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Dinámica de poblaciones y crecimiento de los pastos marinos caribeños Thalassia testudinum Banks ex König, Syringodium filiforme Kütz. y Halodule wrightii Ascherson.

FALLA DE ORIGEN

T E S I S

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Esta tesis se la dedico a mi hijo Ayax

Resumen

Se estudió la dinámica poblacional de las especies de angiospermas marinas *Thalassia testudinum* Banks ex König, *Syringodium filiforme* Kütz. y *Halodule wrightii* Ascherson, que crecen en el Caribe Mexicano. Se realizaron cinco campañas durante tres años consecutivos, en las cuales se obtuvieron los datos de la dinámica de las tres especies utilizando la técnica de determinación de la edad.

Se describen los fundamentos de la técnica de determinación de la edad, así como los cálculos implicados en su aplicación y se demuestra su viabilidad en la cuantificación de procesos ecológicos como demografía de las plantas, producción de hojas y rizomas, intensidad de floración, tasas de mortalidad, reclutamiento, colonización y expansión así como la respuesta de los pastos marinos a ciertas perturbaciones ambientales.

Se presentan y discuten los datos obtenidos de biomasa y dinámica de los haces, crecimiento de los rizomas, intensidad y porcentajes de floración, así como las tasas de mortalidad y reclutamiento de cuatro poblaciones monoespecíficas de *Thalassia testudinum* que se desarrollan en distintas condiciones de exposición al oleaje. También se analizan los datos obtenidos en las comunidades que forman las especies *Syringodium filiforme* y *Halodule wrightii* que crecen en la laguna arrecifal.

Estos resultados permiten señalar que las tres especies de pastos marinos del Caribe Mexicano desarrollan praderas monoespecíficas altamente productivas y los valores de la longevidad de sus haces y la tasa de renovación de sus rizomas, son las que las definen como especies pioneras en el caso de *Syringodium filiforme* y *Halodule wrightii*, y de especie clímax en el de *Thalassia testudinum*.

Las diferencias en los valores de intensidad de floración y crecimiento del rizoma de las especies *Syringodium filiforme* y *Halodule wrightii*, así como en la longevidad de los haces de las tres especies, permiten proponer que *Syringodium filiforme* ocupa una posición intermedia entre *Thalassia testudinum* y *Halodule wrightii* en la dinámica sucesional de los pastos marinos en el Caribe Méxicano.

Estructura de la tesis

La tesis se presenta en la modalidad de artículos publicados, de acuerdo con los lineamientos marcados en el programa del Doctorado. Los artículos van acompañados de un resumen en español de todo el trabajo. Se inicia con una introducción general en donde se plantea el marco teórico y justificación del trabajo, se describe la metodología utilizada así como los objetivos generales, y se concluye con los resultados finales y discusión.

Los objetivos particulares, la metodología utilizada y los resultados obtenidos en cada una de las poblaciones analizadas de las especies *Thalassia testudinum* Banks ex König, *Syringodium filiforme* Kütz. y *Halodule wrightii* Ascherson, se discuten ampliamente en las cinco publicaciones científicas, las cuales se presentan de acuerdo a su fecha de publicación, aunque la mayoría de los datos fueron obtenidos simultáneamente durante las campañas realizadas entre los años 1991 y 1993 en la zona arrecifal de Puerto Morelos, Bahía Mujeres y Laguna de Nichupté, Quintana Roo, México.

Introducción

Las angiospermas marinas son plantas clonales que forman extensas comunidades altamente productivas en las costas de todos los mares, excepto en las zonas polares (den Hartog 1970). Las angiospermas marinas que son capaces de completar su ciclo de vida en el mar, constituyen un número muy reducido de especies que están agrupadas en doce géneros, pertenecientes a dos familias; Potamogetonaceae e Hydrocharitaceae del orden Helobiae (den hartog 1970). No se puede atribuir que su escasa diversidad se deba a que tienen un origen reciente, ya que de ambas familias existen registros fósiles desde el Cretácico (Taktajhan 1959, Phillips y Meñez 1988), época en que también aparecen las primeras formas clonales de angiospermas herbáceas terrestres (Tiffney y Niklas 1985). El registro fósil señala que las angiospermas se originaron en el medio terrestre durante el Jurásico (Taktajhan 1959, Cronquist 1985) pero al retornar al mar se encontraron con importantes restricciones, lo cual ocasionó que sólo algunas, del gran número de formas y estrategias de vida desarrolladas por las angiospermas, pudieran tener éxito en el medio marino (den Hartog 1970, Duarte et al 1994).

La gran homogeneidad funcional y morfológica de las angiospermas marinas explica su escasa diversidad (den Hartog 1970, Tomlinson 1974). Estas especies se caracterizan porque todas son clonales y colonizan el espacio creciendo vegetativamente, la mayoría tienen hojas lineales con meristemos basales, sus tejidos están menos lignificados y su sistema vascular es menos eficiente que el de las angiospermas terrestres (Tomlinson 1974, Stevenson 1988). La uniformidad taxonómica de las angiospermas marinas, sugiere que su arquitectura juega un papel muy importante en su capacidad adaptativa (den Hartog 1970, Tomlinson 1974, Duarte 1991). Por lo tanto, el estudio de su arquitectura proporciona valiosos elementos para predecir su comportamiento ecológico (Patriquin 1973, Duarte 1991).

Las angiospermas marinas son organismos modulares con una arquitectura altamente estructurada. Se denomina "genet" (Kays y Harper 1974, Sarukhán y Harper 1973) al individuo genético producido por un cigoto el cuál esta constituido por un conjunto de subunidades genéticamente idénticas llamadas "ramets" (i.e. hojas flores, internodos de rizoma y raíces, White, 1979), las cuales son las unidades básicas de construcción del individuo genético. Estas unidades son entidades fisiológicas capaces de sobrevivir y morir de manera independiente (Cook 1979) y su tipo de construcción tiene distintas consecuencias en los aspectos de crecimiento, reproducción y sobrevivencia. En algunos casos estas subunidades pueden formar raíces y separarse de la planta original y llevar una vida independiente lo cual plantea el problema de reconocer la identidad del individuo (Jansen 1977).

Duarte (1991) señala que existen estrechas relaciones entre el tamaño y la dinámica de los módulos de las angiospermas marinas, las cuales demuestran la importancia que tiene la arquitectura en su productividad, y también permite explicar los diferentes papeles ecológicos de las especies pequeñas como especies pioneras, y de las grandes como especies clímax. El crecimiento clonal permite que la planta se desplaze, colonice y explore nuevas áreas sin depender exclusivamente del éxito de la reproducción sexual (Schmidt 1990). El crecimiento clonal por tanto tiene importantes implicaciones ecológicas.

El crecimiento de las plantas clonales se lleva a cabo mediante la iteración de sus módulos. La iteración de los módulos les permite a las plantas clonales desarrollar poblaciones extensas y longevas, potencialmente inmortales, a partir de un solo genet, así como ocupar ambientes muy diversos. Los meristemos activos o latentes de las plantas siempre están disponibles para continuar la producción de unidades estructurales (Watkinson y White 1985). Las plantas clonales a diferencia de las plantas aclonales, tienen la capacidad de crecer horizontalmente aumentando su tamaño de manera indefinida, sin presentar limitaciones biomecánicas que limiten su crecimiento (Watkinson y White 1985).

El desarrollo de las plantas clonales esta regulado por su arquitectura, cuyos patrones y reglas de crecimiento están basados en el tamaño de los módulos y en la velocidad con la que se adicionan nuevos módulos. Los patrones de crecimiento están escalados al tamaño de la planta y por tanto la dinámica de los módulos depende de su propia medida (Duarte 1991). La tasa de aparición, la tasa de renovación o la longevidad de los módulos es más rápida y corta en las plantas pequeñas que en las grandes (Duarte 1991).

Los patrones de crecimiento del rizoma, que es la parte de la planta encargada de la expansión (horizontal y vertical) del clon, están basados en la frecuencia de ramificación (i.e. ángulo de desviación de la dirección del crecimiento parental, frecuencia de ramificación) y la distancia a la que el ramet parental coloca el ramet hijo (e.g. Tomlinson 1974, Bell y Tomlinson 1980). El patrón de crecimiento del rizoma determina la ocupación del espacio por la planta y es por tanto, una característica fundamental para la modelización de su dinámica. Las diferencias en los patrones de crecimiento del rizoma determinan la capacidad de expansión (colonización) de los clones y condicionan su papel como especies pioneras y clímax.

Los patrones de crecimiento determinan también las diferencias en la productividad y longevidad de las especies. Los distintos tamaños de los módulos de las angiospermas marinas permiten explicar las diferencias observadas en la dinámica de las distintas especies (Duarte 1991). En el caso de las angiospermas marinas el tamaño de los internodos del rizoma presentan poca plasticidad fenotípica y genotípica dentro de la especie, lo cual permite utilizarlo para caracterizar a las especies (Duarte 1991). La transferencia de substancias entre módulos esta determinado por el diámetro del rizoma, por lo que su tamaño es importante en la integración fisiológica de la planta. Teóricamente los rizomas más gruesos permiten una integración fisiológica entre módulos distantes que las especies con rizomas delgados, lo cual les permite construir módulos mayores (Duarte 1991).

Los patrones de crecimiento de las plantas modulares representan las distintas formas en que es capturado el espacio y espacio corresponde en un amplio sentido a recurso (Harper 1985).

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Las plantas clonales pueden crecer en distintas condiciones ambientales en donde la distribución de recursos no es homogénea debido ya sea a perturbaciones, o como resultado del crecimiento de las plantas (Sutherland 1987). Las plantas responden a esta variabilidad ambiental modificando el arreglo morfológico de sus módulos (Franco 1986), ya que la explotación y utilización de los recursos por las plantas, depende de su habilidad para hacer rápidos ajustes fisiológicos (Kays y Harper 1974). La forma representa una manera de explotar los recursos espacialmente distribuidos, su variación en la arquitectura refleja diferencias en la distribución de los recursos o bien diferencias en la forma de explotarlos (Waller y Steingraber, 1985).

Los cambios ambientales también determinan variaciones en los patrones de crecimiento de las poblaciones modulares y en sus estrategias de ocupación del espacio. El grado en que estos pueden variar depende de la especie (Cook 1985, Alpert 1991). Lovett-Doust (1981) distinguió dos extremos morfológicos representados por las formas "guerrilla y "falange". En el primer tipo los genets se ramifican poco, tienen internodos de rizoma muy largos de manera que quedan muy separados entre si, su expansión es muy rápida y son capaces de colonizar grandes extensiones de terreno. Las especies con forma de crecimiento del tipo "falange" son especies de expansión lenta, con haces más agrupados con una mayor ramificación de los rizomas e internodos cortos. Duarte (1991) sugiere que las diferencias en la plasticidad fenotípica entre las especies de angiospermas marinas, esta asociada a las diferencias en el diámetro de sus rizomas. Las especies con rizomas gruesos pueden utilizar los recursos elaborados en módulos más distantes para producir nuevos módulos, lo cual no hacen las especies con rizomas delgados, que por lo tanto han de ser más dependientes de los recursos disponibles en el espacio físico ocupado por el ramet (Tomasko y Dawes 1989).

Muchas plantas clonales como las de dunas y la mayoría de las angiospermas marinas, crecen en áreas con gran movilidad de sedimentos lo que las hace estar sujetas a enterramiento, lo cual ocasiona una alteración de su patrón de crecimiento (Disraeli, 1984, Marbà et al. 1994). Las plantas que habitan en estos ambientes tienen rizomas verticales que les permiten sobrevivir a cambios moderados en la dinámica de sedimentos (Disraeli 1984, Maun y Lapierre

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1984). Existen varios estudios de la acción de la dinámica sedimentaria en los patrones de crecimiento en plantas de dunas, pero son pocas las evaluaciones cuantitativas de la dinámica de sedimentos en las angiospermas marinas (Patriquin 1973, Boudoresque et al. 1984). Marbà et al. (1994) observaron que existe un estrecho acoplamiento entre la dinámica de crecimiento de la angiosperma marina Cymodocea nodosa y la dinámica sedimentaria en el Delta del Ebro, lo cual permite utilizarlas como trazadores biológicos de la dinámica de sedimentos.

La capacidad de las plantas clonales para sobrevivir al efecto de las perturbaciones dependen del patrón de colonización de la especie y de las características de la perturbación. Con frecuencia, las poblaciones vegetales sufren la acción repetida de perturbaciones a lo largo de su vida, y esto les obliga a mantenerse constantemente recolonizando las zonas perturbadas (Duarte y Sand-Jensen 1990b, Marbà et al 1994). Las poblaciones clonales que pueden sobrevivir al paso de perturbaciones periódicas, son las que puedan crecer a una tasa similar o mayor que la velocidad de la perturbación, o las que tienen un crecimiento más lento que la frecuencia de la perturbación, ya que tienen el tiempo suficiente para cerrar su ciclo de vida (Duarte y Sand-Jensen 1990b). El paso periódico de perturbaciones sobre las poblaciones clonales con estrategias de vida que les permitan sobrevivir a la perturbación, mantienen el proceso de colonización de estas poblaciones en equilibrio dinámico, estableciéndose un estrecho acoplamiento entre la dinámica de la población y la dinámica de la perturbación (Duarte y Sand-Jensen 1990a, Duarte 1991).

En el estudio de dinámica de poblaciones en organismos modulares se reconocen dos niveles de organización; la que se refiere al número de genets (productos de cigotos o una sola célula) y la relativa al número de módulos que componen cada genet. Los cigotos de las plantas modulares desarrollan clones que por sí solos tiene todas las propiedades de una población. Harper (1977), reconoció que las unidades modulares podían ser tratadas y por lo tanto analizadas, como miembros de una población. Si el crecimiento de un genet puede ser descrito en términos de la dinámica de poblaciones de los módulos, entonces a éstos se les pueden asignar atributos poblacionales propios y su crecimiento puede considerarse como un proceso

demográfico (Harper 1980). El estudio demográfico de las poblaciones clonales por tanto permite predecir el crecimiento y el tamaño de una población a partir de la dinámica (i.e. tasa de nacimiento y mortalidad de los ramets) y de la estructura de edad de los ramets, sin tomar en cuenta si el origen de los ramets es vegetativo o reproductivo (Watkinson y White 1986).

Hasta ahora, el conocimiento de la dinámica de los pastos marinos estaba limitado por la lentitud para determinar su edad debido a que la metodología utilizada requería el seguimiento de una población, durante un año como mínimo. La construcción modular y organizada de las hierbas marinas, permitió desarrollar una metodología para reconstruir su dinámica a escalas temporales equivalentes a la longevidad de sus ramets, realizando una sola visita a la población (Duarte et al. 1994). Se postula por lo tanto, que el conocimiento de la dinámica de las angiospermas marinas se puede obtener utilizando los módulos como unidad de análisis.

Los pastos marinos crecen a partir de la iteración de sus módulos básicos los cuales son: (1) los internodos de rizoma, con los cuales la planta asegura su extensión vegetativa y que pueden ser horizontales (en los llamados haces largos) ó erectos (en los llamados haces verticales), dependiendo de si estos extienden la planta hacia los lados o hacia arriba; (2) las hojas, en las cuales se realiza la fotosíntesis y la captación de los nutrientes de la columna de agua, y (3) las raíces, que son el sistema de anclaje de la planta y de toma de nutrientes del sedimento, las cuales aparecen también a intervalos regulares a lo largo del rizoma horizontal. Los puntos de inserción de las hojas en el rizoma son llamados nodos, y son fácilmente identificables por las cicatrices que quedan después de la abscisión de las hojas (Fig. 1). Las piezas del rizoma formadas entre dos cicatrices consecutivas son llamadas internodos de rizoma. Estos internodos se producen durante el intervalo de tiempo que transcurre entre la formación de dos hojas sucesivas, el cuál es llamado Intervalo de Plastocrono (Erickson and Michelini 1957). Esta arquitectura modular de los pastos marinos asegura una relación muy estrecha (1:1) entre la producción de internodos de rizoma y hojas, y constituye la base para la determinación de la edad de los haces y rizomas de los pastos marinos.

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La edad de un haz (i.e. rizoma vertical) en los pastos marinos se puede calcular como el número total de cicatrices (o internodos) de las hojas producidas desde la aparición de los haces o rizomas, más las hojas presentes en el haz. La unidad básica de tiempo para estimar la edad resulta de esta manera ser el Intervalo de Plastocrono, el cual se propone que representa el ritmo interno de crecimiento de la plantas, y con él se pueden obtener estimaciones del "tiempo biológico" (Erickson and Michelini 1957, Lamoreaux et al. 1978, Brouns 1985). Estas unidades de tiempo son específicas de cada especie (cf. Duarte 1991) y requieren ser traducidas a tiempos absolutos (e.g. días) para poder expresar sus tasas de crecimiento. Para traducir el intervalo de plastocrono a unidades de tiempo absoluto se asume una linearidad entre las dos unidades de tiempo (Erickson and Michelini 1957, Patriquin 1973). La duración media anual en días de un intervalo de plastocrono (IP) es una característica de cada especie, como se ha reflejado en la gran variación que hay entre especies comparada a la que existe dentro de la misma especie (Duarte 1991). Sin embargo, dentro de las especies existe también una variabilidad considerable en el IP como resultado de las diferencias entre poblaciones y de la variabilidad a escalas de tiempo interanuales y estacionales. Por lo tanto, para obtener estimaciones confiables de la edad de los pastos se deben realizar mediciones de la duración del IP en distintas poblaciones. El conocimiento de la duración media anual de los Intervalos de Plastocrono puede usarse como una primera aproximación para traducir los IP en tiempo absoluto, y conocer así la dinámica clonal y el crecimiento de las poblaciones de angiospermas marinas.

El objetivo general de este estudio fue analizar la dinámica de las comunidades de *Thalassia testudinum, Syringodium filiforme y Halodule wrightii* que crecen en la zona comprendida entre Puerto Morelos e Isla Mujeres, Quintana Roo, México. La información obtenida nos permitió conocer los valores de densidad y biomasa de los haces verticales y rizomas, la tasa de crecimiento tanto vertical como horizontal de las tres especies, así como sus tasas de mortalidad, reclutamiento y floración.

Para alcanzar este objetivo se partió de las técnicas delineadas por Patriquin (1973) y Duarte y Sand-Jensen (1990a,b) las cuales se emplearon críticamente y se mejoraron para permitir el cálculo del intervalo de plastocrono de todas las poblaciones de las tres especies analizadas, determinar su estructura de edad y dinámica demográfica, y las tasas de crecimiento y renovación de hojas, haces verticales, y rizomas horizontales de las tres especies. También se analizó el esfuerzo reproductivo y se dedujo la frecuencia de floración en las tres especies. Con esta información se realizó el análisis comparativo de la dinámica de las praderas monoespecíficas de las tres especies, y se explicó el papel de *Thalassia testudinum* como especie clímax y de *Syringodium filiforme* y *Halodule wrightii* como especies pioneras. Paralelamente se analizó el contenido de los principales nutrientes en las hojas de *Thalassia testudinum* en las distintas localidades, para tratar de dilucidar si existían limitación por carencia de nutrientes en su crecimiento.

Esta información nos permite incrementar nuestro conocimiento sobre la dinámica de las comunidades de pastos marinos en los ecosistemas costeros mexicanos, con la cuál podremos plantear en un futuro, estrategias de manejo, conservación o recuperación de áreas de pastos marinos devastadas o impactadas.

Figura 1. Morfología modular de los pastos marinos.

Resultados y discusión

Los resultados de las investigaciones acerca de la dinámica, demografía y aspectos reproductivos de las comunidades de las tres especies de pastos marinos que se desarrollan en el caribe mexicano y que se presentaron en cinco publicaciones científicas, son de manera resumida las siguientes:

Se propone y válida una metodología, basada en la formalización de las ideas de Patriquin (1973) y Duarte y Sand-Jensen (1990 a, b) para estimar y reconstruir la dinámica del crecimiento vertical y horizontal de las comunidades de pastos marinos.

Se reporta por primera vez la intensidad de floración de las especies de pastos en las costas de Puerto Morelos, Quintana Roo, en el Caribe Mexicano. Solo el 17 % de los rizomas verticales (también llamados haces) de las plantas de *Thalassia testudinum* florecen en esta zona, y la probabilidad de que lo hagan aumenta tras un período de maduración sexual de aproximadamente dos años. La frecuencia media de floración para la población analizada se estimó en 5.6 10^{-3} flores por intervalo de plastocrono (IP^{-1}), el cuál corresponde en promedio, a un evento de floración cada 13 años. La reconstrucción de la intensidad de la floración en *Thalassia testudinum* en los años previos al paso del Huracán Gilberto, mostró un incremento en 4 veces más después del paso de éste (en Septiembre de 1988). El Huracán Gilberto causó una perturbación substancial a las praderas de pastos marinos, mostrando con ello la importancia de las perturbaciones en la variabilidad interanual de la intensidad de floración. La comparación de la intensidad de floración observada con los datos publicados para otras especies de pastos marinos, sugiere que las diferencias en la intensidad de la floración entre especies, (la cual en promedio es que florecen cada año 10% de los haces), son pequeñas y probablemente no mayores que la variabilidad entre años o entre las poblaciones de las distintas especies.

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Syringodium filiforme y *Halodule wrightii* también requieren de un período de maduración sexual, el cuál es de poco más de un año (8.4 ± 0.8 IP y 29.3 ± 2.7 IP respectivamente) y se encontró que tienen una densidad de haces que florecen de 10 a 50 veces más (300 y 1500 haces con flores m^{-2} respectivamente) que la de *Thalassia testudinum* (las poblaciones examinadas tuvieron un rango de 36 a 94 haces con flores m^{-2}) lo cual incrementa o contribuye a la habilidad de estas especies para colonizar sedimentos sin vegetación más rápido que las especies clímax.

Las praderas de *Thalassia testudinum* de Puerto Morelos, son extraordinariamente productivas (tienen un rango de 1500 a 4500 g de Peso Seco m^{-2} año^{-1}). El 10% de la producción corresponde a los rizomas los cuales tienen una longevidad de entre 6 y 9 años. Los datos de biomasa y producción de *Syringodium filiforme* y *Halodule wrightii* demostraron que estas especies son capaces de desarrollar también praderas muy densas y que mantienen biomasas mayores a los 500 g PS m^{-2} con una producción de hasta 2000 g PS m^{-2} año^{-1} similares a las de *Thalassia testudinum*.

Se encontró que la producción parece estar fuertemente controlada por nutrientes, fundamentalmente por la disponibilidad de fósforo ya que la relación C:P de las hojas (i.e. 618) de *Thalassia testudinum* esta por encima de los valores que indican limitación por fósforo (Fourqueran 1992, Duarte 1991, Short 1993).

Las dos poblaciones de *Syringodium filiforme* y *Halodule wrightii* estudiadas, tuvieron unas tasas de crecimiento horizontal mayores que las reportadas para la zona Norte del Golfo de México (Eleuterius 1987), aunque *Syringodium filiforme* creció a tasas similares a las reportadas para Indian River Lagoon (Florida, USA; Short et al. 1993). Estas especies produjeron más de 2000 g PS m^{-2} debido a sus elevadas tasas de renovación de las hojas (5.0 - 8.5 año^{-1}) y rizomas (2.0 - 3.3 año^{-1}).

Las poblaciones de *Syringodium filiforme* y *Halodule wrightii* además de tener tasas de crecimiento muy altas tienen una gran capacidad de ramificación ya que producen una rama cada

94 y 21.8 cm. respectivamente. Por su parte *T. testudinum* produce una rama por cada 6300 cm de rizoma horizontal. Estas altas tasas de crecimiento y ramificación del rizoma de *Syringodium filiforme y Halodule wrightii* les permite ocupar rápidamente el espacio colonizado. La rápida renovación del rizoma implica sin embargo, una alta tasa de mortalidad de haces y una baja esperanza de vida (la esperanza de vida promedio de los haces es de 100 - 180 días) comparado con *T. testudinum*.

Se encontró que las praderas de *T. testudinum* responden a la dinámica sedimentaria variando la tasa de crecimiento de los haces verticales, y que este crecimiento vertical refleja, por un lado, la estacionalidad de los pastos marinos y, por otro, su respuesta a perturbaciones producidas por huracanes y tormentas tropicales. El promedio de la longitud internodal (en los haces verticales) varió entre 0.17 y 12.75 mm. y fue mayor en las praderas que experimentaron el mayor enterramiento por las olas de arena desplazadas por el Huracán Gilberto. La longitud promedio de los internodos mostró diferencias interanuales importantes como resultado de las perturbaciones derivadas del paso del Huracán Gilberto. La longitud internodal mostró ciclos anuales que se confirmaron con la presencia de las cicatrices florales que precedían o coincidían con los valores mínimos anuales de longitud internodal. La presencia de estos ciclos anuales en los haces permitieron la estimación de la producción foliar anual de *T. testudinum*, la cual varió en promedio, de 14.2 a 19.3 hojas haz^{-1} año^{-1} en las diferentes áreas estudiadas. Un mayor crecimiento vertical de los haces estuvo asociado a internodos mas largos y tasas de producción foliar más altas, alcanzando valores máximos de aproximadamente 25 hojas haz^{-1} año^{-1} con un crecimiento vertical de 30 mm año^{-1}.

La variabilidad en el crecimiento vertical de los haces de *T. testudinum* puede atribuirse: a) cambios estacionales en el crecimiento de las plantas y b) una variabilidad a largo plazo asociado a perturbaciones episódicas relacionadas con la redistribución de sedimentos por los huracanes y tormentas tropicales. Como consecuencia, la variabilidad en el crecimiento vertical esta muy relacionada a los cambios en la dinámica de los sedimentos.

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A partir de la estructura de edad de las poblaciones se calcularon las tasas de mortalidad y reclutamiento de los haces, y las tasas de renovación de los rizomas verticales, los cuales son indicativos de las tasas de mortalidad y reclutamiento de los rizomas horizontales. El tiempo máximo de vida calculado para los haces de *Thalassia testudinum* varió entre 6 y 9 años, la tasa de reclutamiento es de 0.28 a 1.35 unidades ln por año y una tasa de mortalidad promedio de 0.75 unidades ln por año. Los haces se renuevan a una tasa de 0.6 año^{-1}, lo cual representa también la tasa de renovación del rizoma. El promedio de esperanza de vida de los haces de *Syringodium filiforme* y *Halodule wrightii* fue respectivamente de 0.6 y 0.3 años, y las tasas de reclutamiento fueron 0.77 y 4.18 unidades ln año^{-1} y las de mortalidad 2.04 y 3.54 unidades ln año^{-1} respectivamente. Esto significa que, a pesar de que estas especies pioneras son capaces de ocupar rápidamente el espacio que colonizan, los haces una vez establecidos no pueden permanecer ocupando el espacio durante tanto tiempo como lo pueden hacer los de especies mas longevas como *Thalassia testudinum*. Sugerimos por lo tanto, que el papel de las especies de pastos marinos como especies pioneras, o como especies clímax, es independiente de su capacidad de desarrollar poblaciones densas y productivas y esta más relacionado con la longevidad de sus haces y la tasa de renovación de sus rizomas.

La elevada tasa de crecimiento asociada a la alta tasa de mortalidad de *Syringodium filiforme* y *Halodule wrightii* implica que estas especies pioneras deben tener grandes requerimientos de nutrientes (Fourqueran et al. 1992, Short et al. 1993, Duarte et al. 1994). La rápida pérdida del material de *Syringodium filiforme* y *Halodule wrightii*, el cuál constituye la mayor parte del abundante material de pasto marino que es arrojado a la playa, asociado al corto ciclo de vida de sus hojas y haces, seguramente reducen su capacidad de almacenamiento y reciclaje interno de nutrientes. En contraste *Thalassia testudinum* crece mas lentamente y vive más tiempo (Gallegos et al. 1993), y por lo tanto debe tener menor requerimiento de nutrientes (Fourqueran et al 1992, Duarte 1994), y debe tener una mayor capacidad para almacenar y reciclar los nutrientes (Patriquin 1972).

Estas observaciones ayudan a explicar porqué *Thalassia testudinum* es la especie clímax en el Caribe y porqué las densas praderas desarrolladas por *Syringodium filiforme* y *Halodule wrightii* son reemplazadas eventualmente por praderas de especies clímax (den Hartog 1971, Williams 1987). Nuestros resultados demuestran también importantes diferencias en el potencial reproductivo y en el crecimiento del rizoma de las dos especies pioneras. La densidad de haces que florecen en *Halodule wrightii* fue 5 veces mayor que en *Syringodium filiforme*, el cuál tuvo también una tasa de renovación y de crecimiento menores. Por lo tanto se propone que *Syringodium filiforme* tiene una posición intermedia en esfuerzo reproductivo, renovación de rizoma y longevidad de sus haces, entre *Halodule wrightii* y *Thalassia testudinum*, por lo que también ocupa una posición intermedia en la secuencia sucesional de los pastos marinos en el Caribe.

Los resultados presentados aquí demuestran que la técnica de la determinación de la edad tiene un gran potencial, ya que permitió cuantificar la dinámica de las especies de pastos marinos que se desarrollan en el Caribe Mexicano y describir los principales mecanismos que regulan su funcionamiento.

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TESIS SIN PAGINACION

COMPLETA LA INFORMACION

Flowering of *Thalassia testudinum* Banks ex König in the Mexican Caribbean: age-dependence and interannual variability

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ABSTRACT

Gallegos, M.E., Merino, M., Marbá, N. and Duarte, C.M., 1992. Flowering of *Thalassia testudinum* Banks ex König in the Mexican Caribbean: age-dependence and interannual variability. *Aquat. Bot.*, 43: 249–255.

The flowering intensity of *Thalassia testudinum* Banks ex König, along the Mexican Caribbean coast, was studied. Only 17% of the shoots examined had flowered during their lives, and the mean flowering frequency for the population was estimated to be 5.6×10^{-3} flowers per plastochrone interval (PI^{-1}), which corresponds, on average, to a flowering event every 13 years. Thus, most short shoots will not flower during their lives, although some old shoots had flowered twice and even three times. None of the shoots examined flowered before reaching an age of 15 PI (about 1 year), and flowering intensity increased with age up to 30 PI (about 2 years), thereby indicating the need for sexual maturation. Reconstruction of the flowering intensity in previous years showed a four-fold increase since the passage of Hurricane Gilbert (in September 1988), which caused substantial perturbation to the seagrass meadows, thereby indicating the importance of perturbation on interannual variability in flowering intensity. Comparison of the flowering intensity observed with published reports for other seagrass species suggests that differences in flowering intensity among species, which averaged about 10% of the shoots flowering each year, are narrow and probably not greater than variability among years or populations of a single species.

INTRODUCTION

Seagrass meadows cover extensive areas of coastal zones in the tropical and temperate zones (Den Hartog, 1970). These important ecosystems often ex-

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perience catastrophic declines, which frequently derive, in tropical areas, from the passage of hurricanes and tropical storms (Birch and Birch, 1984). Because recovery of the meadows from catastrophic decline depends both on sexual reproduction and horizontal growth rate (Duarte and Sand-Jensen, 1990), modelling of the recovery process requires explicit knowledge of both processes. Whereas data on horizontal growth rates of seagrass species are relatively abundant (see Duarte, 1991), data on the reproductive effort of seagrass species are sparse (e.g. Johnson and Williams, 1982; Caye and Meinesz, 1985; Durako and Moffler, 1987; Hootsmans et al., 1987; Gambi, 1988; Pergent and Pergent-Martini, 1990).

Here we determine the flowering intensity of *Thalassia testudinum* Banks ex König along the Mexican Caribbean coast, where it dominates seagrass meadows. We also assess the age-dependence of flowering events and examine the changes in the frequency of sexual reproduction after passage of hurricane Gilbert (with wind speeds up to 300 km h^{-1}; Merino and Otero, 1991), which caused a major disturbance to the seagrass beds of the studied area (Marbá et al., unpublished data, 1992).

MATERIALS AND METHODS

Flowering frequency and age of short shoots were studied in a *T. testudinum* meadow at Puerto Morelos (20°51'N, 86°55'W), Quintana Roo, on the eastern coast of the Yucatan Peninsula, Mexico. The meadow studied grows at −3.0 m along the beach of the lagoon formed by a barrier reef running parallel to the coast (Merino and Otero, 1991). We randomly collected (between 20 and 24 August 1991) 308 short shoots from the population, using a 20.5 cm internal diameter corer (total 24 samples) driven 40 cm into the sediment to collect the shoots down to their rhizomes (buried about 10 cm in the sediment). Sediment (coarse carbonated sand) was carefully rinsed out of the sample, and shoots that had lost their connection to the rhizome, and, consequently, could not be aged (<10%), were discarded. The age of a shoot was measured as the total number of leaves produced during its life (i.e. number of leaf scars + number of standing leaves; Patriquin, 1973; Cox and Tomlinson, 1988). The resulting time units correspond to the average time interval between the initiation of two successive leaves on a shoot, referred to as plastochrone interval (PI) (Erickson and Michelini, 1957; Brouns, 1985a,b). Plastochrone intervals represent indirect estimates of time, which, although subject to seasonal variability, provide accurate estimates of time at interannual time scales (see Brouns, 1985a,b). Present and past flowering events were identified visually, if flower peduncles were still standing, or by searching the short shoots for the distinct peduncle scar (see Durako and Moffler, 1987; Cox and Tomlinson, 1988). Shoot age at the time of flowering was measured as the number of leaf scars below the peduncle scar. Plasto-

chrone interval units were translated into natural time using the mean time elapsed between the production of successive leaves for this population (26.1 days; Marbá et al., unpublished data, 1992), thereby allowing reconstruction of flowering events in past years.

RESULTS AND DISCUSSION

Only 17% of the shoots examined had flowered, some of them more than once, resulting in a total of 65 flowering events for the 308 shoots examined. Because the 308 shoots examined had produced a total of 11 508 leaves (i.e. PI) during their lives the 65 flowering events represent an average flowering frequency of 5.6×10^{-3} flowers per plastochrone interval (PI^{-1}) (i.e. 65/ 11 508) for the population examined. Because the average leaf production rate of the population examined is 14 leaves per year (Marbá et al., unpublished data, 1992), this means that, on average, a shoot will only flower once every 13 years (i.e. $(14 \text{ PI per shoot year}^{-1} \cdot 5.6 \times 10^{-3} \text{ flowers } PI^{-1})^{-1}$), or that only one of every 13 shoots will flower in a particular year. Because the average life expectancy of the short shoots is 21 PI (Gallegos et al., unpublished data, 1992), our results imply that most short shoots will not flower during their lives. However, nine shoots were observed to flower twice and two even flowered three times, supporting previous reports (Durako and Moffler, 1987; Cox and Tomlinson, 1988) that *T. testudinum* shoots may flower more than once. Examination of the time elapsed between successive flowering events in individual shoots showed this to be multiples of 16.9 ± 0.66 leaf PI, which is close to the average leaf production rate for the population studied (14 leaves year^{-1}; Marbá et al., unpublished data, 1992).

Examination of shoot age structure (Fig. 1a) showed an exponential decrease in shoot abundance, with shoot age indicative of an exponential mortality process (about 0.05 natural log units year^{-1}; Gallegos et al., unpublished data, 1992). Examination of shoot age at the time of flowering (Fig. 1b) showed that none of the shoots flowered before reaching an age of 15 PI (about 1 year), thus indicating the need for a period of sexual maturation before the shoots were capable of sexual reproduction. The decline in flowering events observed as shoot age increases (Fig. 1b) may reflect either a decline in sexual effort with shoot age or may simply reflect the fact that exponential mortality results in there being fewer old than young shoots (Fig. 1a). These possibilities were elucidated by examining the age-dependence of flowering frequency (i.e. the number of flowers produced within a time interval divided by the number of shoots present at that time interval), which showed that flowering frequency increased with increasing age up to 30 PI (about 2 years), and remained rather constant beyond this age (Fig. 1c). Thus, age-dependence of sexual effort in *T. testudinum* is limited, at least in the population examined, to a need to reach an age of about 2 years for full flowering rate to be achieved. Our finding that *T. testudinum* requires 2 years before
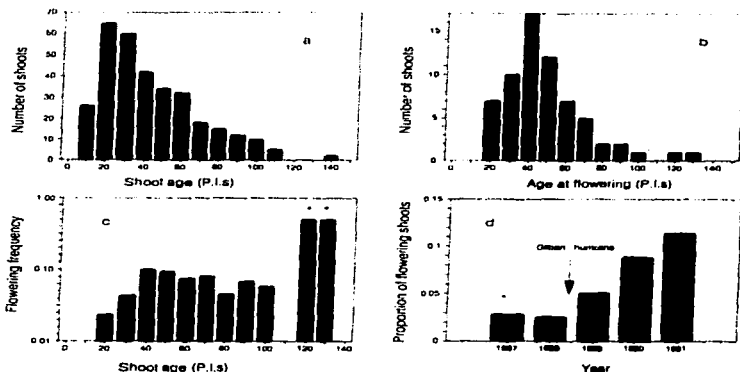
Fig. 1. Flowering intensity of a population of *T. testudinum* Banks ex König in the Mexican Caribbean, as: (a) shoot age structure; (b) the distribution of shoot age at flowering; (c) the relationship between shoot age (in ten plastochrone interval age classes) and the proportion of shoots producing flowers (asterisks represent values for which sample size is less than 3); (d) the interannual (1987–1991) changes in flowering intensity (as the fraction of the shoots that flowered in a particular year) of the population (the asterisk indicates that the estimate for 1987 represents an upper limit on the flowering intensity that year, which could not be accurately calculated because of insufficient sample size). Shoot age is reported in plastochrone intervals (i.e. the average time interval between the initiation of two successive leaves on a shoot: approximately 26.1 days (Marbá et al.. unpublished data, 1992)).

full flowering rate is achieved supports the observation by Thorhaug and Roessler (1977) of a single *T. testudinum* shoot which required 3 years before it was able to flower in Biscayne Bay, Florida.

Reconstruction of flowering intensity (as the proportion of shoots flowering in a particular year; Fig. 1d revealed a steady increase in annual flowering intensity since the passage of hurricane Gilbert (September 1988, i.e. after flowering in 1988, which occurred from March to May), to reach a four-fold higher level in 1991. Hurricane Gilbert severely damaged benthic communities in the Mexican Caribbean (Fenner, 1991), thinning, by uprooting or burying, large areas of the *Thalassia* beds (Marbá et al., unpublished data, 1992). Thus, the increased flowering intensity reported here describes, together with the stimulation of vertical shoot growth and leaf production rate following the passage of hurricane Gilbert (Marbá et al., unpublished data, 1992), the

plant's reaction in response to perturbation. These results demonstrate large changes in flowering intensity between years, which appear to be related, as suggested by Durako and Moffler (1987), to perturbations, such as damage by hurricanes.

The results presented demonstrate that sexual reproduction in the studied *T. testudinum* population is sparse (only 17% of the shoots flowered eventually). Most short shoots never produce flowers, despite their potential to flower more than once. The reproductive effort observed (i.e. an average of 6.2% flowering shoots year^{-1}; Table 1) is about a third of that reported by Durako and Moffler (1987) for a *T. testudinum* bed in Tampa Bay (FL). The high flowering intensity recorded by Durako and Moffler (1987) is, indeed, the highest value we found in the literature (Table 1). Accounts of flowering intensity for different seagrass species ranged from 3.9 to 17.8% of the shoots, with an average of 9.6%, which is a rather narrow range considering the diverse species examined. Values within species are, however, subject to great variability, representing differences among populations (e.g. Pergent and Pergent-Martini, 1990) and interannual changes (e.g. Fig. 1d), which may be greater than the differences between species. Despite this variability, available data (Table 1) suggest that the differences in flowering intensity between different seagrass species, from that of *Posidonia oceanica* (L.) Delile, the flowering of which has been considered to be "quite a rare phenomenon" (Pergent et al., 1989), to that of *Zostera noltii* Hornemann, which is considered to flower abundantly (Hootsmans et al., 1987), are not as large as perceived in the past. We therefore suggest that the perceived differences in the flowering intensity of large and small seagrasses reflect differences in their abundance (i.e. shoot density) imposed by their size (Duarte and Kalff,

TABLE 1

Literature reports (average values and range) of flowering intensity in different seagrass species

Species	Proportion of shoots flowering (%)	Reference
Halodule wrightii Aschers.	11.7 (4.7–26.6)	Johnson and Williams (1982)
Syringodium filiforme Kütz.	10.4 (3.8–23.7)	Johnson and Williams (1982)
Thalassia testudinum Banks ex König	17.8 (10.0–29.4)	Durako and Moffler (1987)
T. testudinum Banks ex König	6.2 (3.0–11.4)	Present study
Zostera noltii Hornemann	4.7 (1.3–9.1)	Hootsmans et al. (1987)
Zostera marina L.	3.9 (3.7–4.2)	Sand-Jensen (1975)
Z. marina L.	10	Aioi (1980)
Z. marina L.	12.6 (1.3–24.0)	Roman and Able (1988)
Z. marina L.	14.0 (8.2–20.4)	Ibarra-Obando (1989)
Z. marina L.	7.3	Robertson and Mann (1984)
Cymodocea nodosa (Ucria) Aschers.	5.5	Caye and Meinesz (1985)
Posidonia oceanica (L.) Delile	10.9 (0.4–25.0)	Pergent and Pergent-Martini (1990)
Average overall (range of averages)	9.6 (3.9–17.8)	

1987), rather than differences in their relative flowering frequency (ie. proportion of flowering shoots). The smaller density reached by large seagrasses (Duarte and Kalff, 1987) also means, therefore, that they should produce fewer flowers and fruits per unit area than small species. Yet, the larger size of flowers and fruits of large seagrasses (Duarte, 1991) may balance the areal allocation of resources (as limiting nutrients or matter) allocated to sexual effort (i.e. the product of the size and areal density of reproductive structures) by different seagrass species. The suggestion that the areal density of flowers produced by different seagrass species is likely to be size-dependent, together with the size-dependence of rhizome growth, (Duarte, 1991) suggest the rate of seagrass recovery, should also be size-dependent.

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Biomass and dynamics of *Thalassia testudinum* in the Mexican Caribbean: elucidating rhizome growth

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ABSTRACT: We report here data on biomass and dynamics of shoots and rhizomes of *Thalassia testudinum* in the Mexican Caribbean based, primarily, on aging of plant material. We found *T. testudinum* to be able to reach high biomass (>1000 g dry wt m⁻²) and develop highly productive populations (1500 to 4500 g dry wt m⁻² annually, of which 10 % were allocated to the rhizomes) in the Mexican Caribbean. The plants appeared to grow slowly, as reflected in longer time intervals in between production of leaves and shoots, and slower rhizome elongation rates and leaf production rates than found in the past, possibly as a result of their low nutrient, particularly phosphorus, content. Calculated maximum shoot life spans ranged between 6 and 9 yr, shoot recruitment rates ranged from 0.03 to 0.07 in units per plastochrone interval (PI) and shoot mortality rate was substantial and averaged about 0.045 in units PI⁻¹. Shoots turned over at ca 6 to yr⁻¹, which also represents the rhizome turnover rate.

INTRODUCTION

Shallow areas of the Caribbean Sea are characterised by highly productive seagrass meadows, dominated by *Thalassia testudinum* Banks ex König (den Hartog 1970). Our knowledge of the production of *T. testudinum* is, however, skewed towards populations along the coasts of Florida, USA (e.g. Zieman 1974, Kenworthy & Thayer 84, Zieman et al. 1989), and Caribbean Islands (Patriquin 1973, Buesa 1974, Williams 1988), and there is a need to extend these measurements to *T. testudinum* beds elsewhere in the Caribbean. Moreover, most of the available data on *T. testudinum* production refer to leaf growth, and there is a remarkable paucity of data on growth of *T. testudinum* rhizomes (Duarte 1991). The scarcity of data should be attributable to the greater interest in aboveground production, for simple techniques to estimate growth of *T. testudinum* rhizomes have been available for about 2 decades (Patriquin 1973).

We report here data on biomass and dynamics of 3 different populations of *Thalassia testudinum* in the Mexican Caribbean, with emphasis on growth and dynamics of rhizomes, both vertical (i.e. short shoots) and horizontal. We used biomass measurements and plant aging techniques (Patriquin 1973) to elucidate shoot age structure and population dynamics. Our study of plant growth followed, therefore, a demographic approach, which, although not strictly equivalent to conventional (i.e. based on plant weight) growth analysis, yields comparable results and offers clear operational advantages (McGraw & Garbutt 1990a, b). To compare these results with previous (based on weight) growth analyses, we converted our demographic estimates of plant growth to conventional (i.e. weight-based) units by combining the measured biomass of the different seagrass fractions with their (demographic-based) turnover times.

METHODS

We sampled 3 different *Thalassia testudinum* populations around Cancún (about 21° N, 87° W; Yucatán enínsula, México) subject to different degrees of nthropogenic disturbance. The first population was ext to an undisturbed coral barrier-reef (reef population), the second grew in the reef-lagoon beach (reef-lgoon population), influenced by the nearby town of uerto Morelos, and the third grew in shallow, eutrophied Bojorquez Lagoon (Merino & Otero 1991, Reyes Merino 1991). Previous studies, based on the identification of annual cycles in *T. testudinum* vertical shoot rowth, estimated the annual leaf production rate of iese populations to range from 17 leaves shoot[-1] yr^{-1} the eutrophied lagoon and the barrier reef, to a inimum of 14 leaves shoot[-1] yr^{-1} in the reef-lagoon ach (N. Marbá, M. E. Gallegos, M. Merino, C. M. uarte unpubl.). These estimates refer to annual ents and are, therefore, not necessarily accurate at orter time scales. Because these 3 populations differ aspects other than the anthropogenic influence they e subject to (e.g. exposure to mechanical stress, arbá et al. unpubl.), our goal in studying these 3 populations was to increase the generality of our findings · encompassing a range of conditions, and we do not tempt to attribute observed differences to anthrogenic disturbance.

Shoots and rhizomes of *Thalassia testudinum* were llected in 12 to 24 (depending on plant density) plicated cores (20.5 or 28 cm internal diameter) shed to a depth of about 40 cm in the sediment arse carbonated sand), thereby containing all living izomes. Sediment was carefully rinsed off the nples to prevent shoots from loosing their connec- n to the rhizomes, which was needed to estimate ot age. We then counted all of the living shoots and i internodes of the rhizome pieces in the sample, inted the number and measured the length and dth of all entire leaves in each shoot, and measured length (from their insertion in the rhizome to the swing meristem) of the vertical rhizomes in the short ots. The length of the rhizome pieces in between isecutive shoots was also measured and the number internodes counted to be used to estimate rhizome owth. We then estimated the age of all living (i.e. iting green leaves) and dead (i.e. devoid of green ves) shoots that maintained their connection to the come (> 80 % of the shoots) as the sum of leaf scars I standing leaves (Patriquin 1973). Dead shoots re dated only if they ended in a rounded tip, indi- ng that the shoot was not broken. The resulting ·time units correspond to the average time interval ween the initiation of 2 successive leaves on a ot, referred to as plastochrone interval (PI; Erickson

& Michelini 1957, Brouns 1985a, b). Plastochrone intervals represent indirect estimates of time, which, although subject to seasonal variability, provide accurate estimates of time at interannual time scales (cf. Brouns 1985a, b). A subsample of the shoots and rhizomes in each sample was dried overnight at 70°C to calculate average dry weights of these modules, and leaf nutrient (C, N and P) contents were measured in duplicate subsamples (coefficient of variation of replicate samples < 2 %) using a Carlo-Erba autoanalyzer for C and N contents, and a colorimetric method, following wet acid digestion, for P determinations (Koroleff 1983).

Shoot age structure was represented by the age of both living and dead shoots. Although the average age of living shoots represents the overall age of the shoot population, it does overestimate their average life expectancy, which is best represented by the age at death. The age difference between consecutive shoots along the rhizome was used to estimate the time interval (as plastochrone intervals) in between the appearance of consecutive shoots (hereafter termed shoot plastochrone interval), and the rate of rhizome elongation (i.e. the ratio of the length of the rhizome piece to the age difference, cf. Patriquin 1973). The ratio of the number of rhizome internodes in between consecutive shoots to the age difference between them was used to estimate the rate of appearance of rhizome internodes (Patriquin 1973). Similarly the growth rate of vertical rhizomes was estimated as the slope of a linear regression equation between shoot length of vertical rhizomes (y) and their age (i.e. number of leaf scars, x). All time estimates based on leaf plastochrone intervals (i.e. shoot age, rhizome extension rate, shoot appearance rate) were converted into natural time by using the annual mean duration of the leaf plastochrone interval (26.1, 21.7 and 21.3 d for the reef-lagoon beach, barrier reef and eutrophied lagoon respectively) from Marbá et al. (unpubl.). Shoot mortality (K, in natural logarithm units time[-1]; cf. Duarte & Sand-Jensen 1990b) was calculated from the age distribution of the shoots by fitting the equation

$$N_t = N_0 e^{-Kt} \qquad (1)$$

which describes the exponential decline in shoot number (N) in increasingly old age classes with time (t) from the onset on mortality (t = 0).

RESULTS AND DISCUSSION

All populations had leaves depleted in phosphorus relative to other nutrients (Table 1), suggesting that phosphorus availability probably limits their growth (cf. Duarte 1990), and consistent with the hypothesis

1 carbonated sediments support phosphorus-limited grass meadows (Short 1987). Although the leaves of the in the eutrophied lagoon had higher nitrogen centrations then those of other populations, the re the most depleted in phosphorus relative to bon and nitrogen (Table 1), suggesting that their wth may have been phosphorus limited despite estantial nutrient loading to the lagoon. The popula- in the eutrophied lagoon was denser and had ater shoot biomass than the reef populations ble 1), which also had shoots bearing fewer and rter leaves. Rhizome biomass was also greater at eutrophied lagoon, because of a tendency to have re and longer internodes there than those at the f populations (Table 1), although this difference s much smaller than that in shoot biomass.

Ve observed a close relationship between rhizome mass and shoot density, and between shoot density f shoot biomass (Fig. 1), indicative of a close depen- nce of shoot density and biomass on rhizome devel- ment. Leaf turnover, estimated as the ratio between annual leaf production rate and the average number aves per shoot, was found to be lowest at the eutro- ed lagoon (Table 1). The rate of rhizome growth, ssured as the horizontal elongation rate and the rate

of appearance of rhizome internodes (i.e. rhizome Pl), tended to be greater, but not significantly so. In the reef meadow (Table 1). The rate of appearance of new shoots (i.e. shoot Pl, Table 1) was, however, significantly lower at the reef-lagoon meadow (<2 shoots rhizome apex[-1] yr^{-1}) than those at the reef and the eutrophied lagoon (ca 4 shoots rhizome apex[-1] yr^{-1}). The regression equa- tion describing the relationship between the length (in mm) of the vertical rhizomes (i.e. short shoots) and their age (in leaf Pls) (Fig. 2).

$$\log \text{shoot length} = 0.06 + 1.03 \log \text{shoot age} \quad (2)$$
$$R^2 = 0.80, N = 364, F = 1450, p < 0.0001$$

indicated that the rate of vertical growth of short shoots did not change significantly as shoots became older (i.e. H_0: slope = 1, t-test, p > 0.50). Moreover, analysis of covariance showed the rate of vertical growth of short shoots to be similar, at about 1 mm per leaf produced, for all populations examined (ANCOVA, p < 0.0001; Fig. 2). Substantially faster (up to 10-fold) vertical growths may occur, however, in response to burial (Marba et al. unpubl.). The slope of this relationship (1 mm per leaf produced) indicates a vertical growth of the rhizomes of ca 15 to 20 mm yr^{-1}, which, multiplied by the density of short shoots (500 to 1000 shoots m[-2])

le 1. *Thalassia testudinum.* Summary of the biomass and dynamics of the seagrass populations studied, represented by indisturbed meadow growing next to a barrier reef, a population subject to moderate anthropogenic disturbance (lagoon-reef ch), and a population growing in a eutrophied lagoon (Bojorquez Lagoon). Mean ± SE reported, and F-values and probability ies from 1-way ANOVA to test for significant differences among the populations are reported for all variables, except for those ulated from other variables. *: populations that differed significantly from the others (HSD Tukey multiple comparisons test); NS: not significant

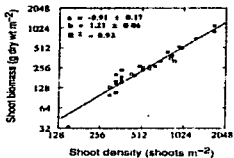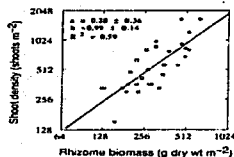| ariable	Reef	Lagoon-reef	Bojorquez L.	F-value
oot biomass (g dry wt m[-2])	222 ± 38	222 ± 22	693 ± 105*	28 (<0.0001)
oot density (shoots m[-2])	480 ± 50	510 ± 54	1722 ± 160*	21 (<0.0001)
af length (mm shoot[-1])	122.2 ± 8.3	109 ± 5.0	256 ± 23.4*	51 (<0.0001)
aves shoot[-1]	2.5 + 0.07	2.3 ± 0.05	2.47 ± 0.07*	34.5 (<0.0001)
izome biomass (g dry wt m[-2])	307 ± 41	261 ± 17	467 ± 47*	6.5 (<0.001)
ernodal length (mm)	5.5 ± 0.2	4.8 ± 0.14	5.9 ± 0.21*	9.3 (<0.001)
ernode density (internodes m[-2])	12800 + 1700	15400 ± 1000	24300 ± 2500*	10 (<0.001)
tal shoot biomass turnover (yr^{-1})	7.3	6.1	5.8	—
izome Pl (d internode[-1])	3.7	5.5	5.4	—
izome elongation (cm yr^{-1})	35 ± 8.9	22.3 ± 3.6	24.4 ± 2.5	1.6 (NS)
oot Pl (d shoot[-1])	84 ± 17	193 ± 44	81 ± 8.5	4.1 (<0.05)
oot age (leaf Pl)	27.7 ± 1.3*	38.8 ± 14*	17.2 ± 1.0*	65 (<0.0001)
oot recruitment (in units Pl[-1])	0.024	0.018	0.069	—
erage shoot life expectancy (leaf Pl)	20.9 ± 1.7	21.2 ± 1.4	16.8 ± 1.5	1.6 (NS)
aximum shoot life expectancy	116 Pl (7 y)	134 Pl (9.5 y)	99 Pl (6 y)	—
oot turnover (yr^{-1}) (= rhizome turnover)	0.48	0.66	0.70	—
izome internodes in between shoots	13.1 ± 0.4	15.4 ± 0.8*	11.6 ± 0.7	9.3 (<0.001)
izome length in between shoots (mm)	69.3 ± 2.2	71.2 ± 2.5	58.4 ± 2.6*	7.9 (<0.001)
oot mortality rate (in units Pl[-1])	0.046 ± 0.004	0.053 ± 0.008	0.040 ± 0.007	NS
rbon (% dry wt)	32.77	34.65	32.79	—
rogen (% dry wt)	2.18	1.78	2.72	—
osphorus (% dry wt)	0.180	0.147	0.139	—
N: P (atoms)	316:29:1	669:29:1	669:47:1	—

Fig. 1. *Thalassia testudinum*. Relationship between rhizome biomass and shoot density, and between shoot density and shoot biomass of seagrass in the reef meadow (o), Bojorquez Lagoon (•), and reef-lagoon beach (□). Relationships are described by the regression coefficients (± SE) of the fitted equation $y = aX^b$, and the coefficient of determination (R^2)

Fig. 2. *Thalassia testudinum*. The relationship between length and age of vertical seagrass shoots in the reef meadow (o), Bojorquez lagoon (•), and reef-lagoon beach (□)

represents between 7.5 and 20 m of vertical rhizome produced m^{-2} yr^{-1}. These figures indicate that vertical growth must represent a sizeable fraction of the biomass produced.

Examination of the age structure of living shoots showed an increase in the abundance of short shoots < 1 yr, which indicates that recruitment was not completed for the present year, and a tendency towards a decline in the abundance of older shoots (Fig. 3), indicative of shoot mortality. The decline in shoot abundance with shoot age was particularly evident for the Bojorquez Lagoon population (Fig. 3), which had, on the average, the youngest shoots (Table 1). These data allowed estimation of recruitment rates, which ranged from 0.02 to 0.07 in units PI^{-1} in the reef populations and the eutrophied lagoon, respectively (Table 1). Because the mean age of living shoots overestimates overall shoot life expectancy, we used the age-at-death of dead shoots to better estimate this. The cores collected included large numbers of dead
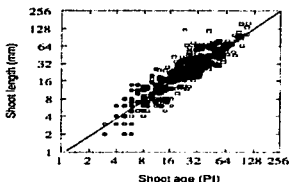
shoots, which lacked standing leaves and ended on a rounded tip resulting from meristem death. Dead shoots outnumbered living shoots in the samples, the number of dead shoots which could be aged (i.e. maintained the connection to the rhizome) alone being larger than that of living shoots. Most shoots died at ca 20 PI (i.e. the average shoot life expectancy), and the average number of leaves produced at death did not differ significantly among shoots of different populations (Table 1). Yet, the longer plastochrone intervals of the reef population imply that their shoots had somewhat longer life expectancies (in days) than those of the remaining populations.

The distribution of shoot age at death (Fig. 3) revealed a clear exponential decline in shoot abundance with increasing shoot age for all 3 populations, thereby allowing accurate calculation of shoot mortality rates compared to those calculated from the distribution of living shoots (Duarte & Sand-Jensen 1990b), which yield biased estimates if shoot recruitment varies substantially among years. The mortality rates calculated from the distribution of shoot age at death averaged about 0.045 in units PI^{-1} (Table 1), similar to the magnitude of calculated recruitment rates (Table 1), and did not differ significantly among populations (t-test, p > 0.10). Our findings indicate that the populations sampled experience essentially similar mortality rates despite differing significantly in shoot age structure (Table 1), which can only be accounted for if recruitment rates varied during the life of the population, increasing in the eutrophied lagoon and decreasing in the reef populations.

The oldest shoots encountered (whether dead or living) had ages between 6 and 9 yr, in agreement with the longevity of 7 yr reported for *Thalassia testudinum* in the Mississippi, USA, area by Eleuterios (1987). For
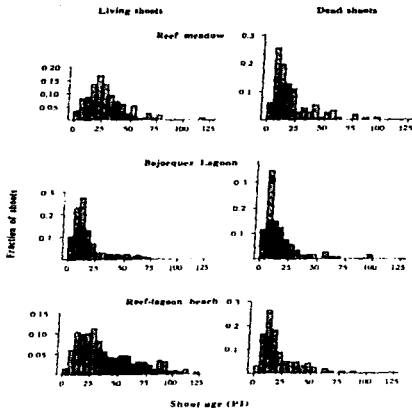
Fig. 3. *Thalassia testudinum*. The age distribution of living and dead seagrass shoots in the populations examined

the populations to remain stable, the turnover time of leaf-bearing rhizomes (i.e. short shoots), which is equivalent to the turnover time of shoot density, should be of the same order as their average life expectancy, (i.e. ca 0.6 yr⁻¹, Table 1). Moreover, recruitment of short shoots should be closely linked to rhizome development (Fig. 1) because the production of new shoots requires, on the average, a fixed investment in rhizome growth, as reflected in the rather uniform number of internodes and length of rhizome produced in between 2 consecutive shoots (Table 1) and the close relationship between rhizome biomass and shoot density (Fig. 1). Thus, turnover rates of vertical (i.e. short shoots) and horizontal rhizomes are expected to be similar (i.e. about 0.6 yr⁻¹, Table 1).

The annual biomass production of the populations can be approximated from our (demographic-based) estimates of leaf and rhizome turnover times (Table 1)

by multiplying these by the biomass of the different compartments. These calculations indicate that the *Thalassia testudinum* populations examined should produce ca 1500 to 4500 g dry wt m⁻² annually, of which 10% represent rhizome production, similar to the 15% reported, based on short-term measurements, by Patriquin (1973). The leaf shoot production calculated represents annual shoot production rates in excess of 6 g dry wt m⁻² d⁻¹, corresponding to leaf turnover rates of about 1.8% d⁻¹ (Table 1). Rhizome growth was slow, as reflected in the long time intervals in between production of shoots and low rhizome elongation rates compared to average values for *T. testudinum* published in the past (Duarte 1991). Yet, *T. testudinum* may produce >30 leaves shoot⁻¹ yr⁻¹ in the Mexican Caribbean (Marbà et al. unpubl.), compared to <20 leaves shoot⁻¹ yr⁻¹ observed in the populations examined here (Table 1), if exposed to high burial, and associated high nutrient supply (Marbà et al. unpubl.).

The results presented showed *Thalassia testudinum* to be able to develop highly productive populations on the mostly oligotrophic Mexican Caribbean coast. Both the biomass and shoot production measured were within the average values reported for this species (Stevenson 1988) (Table 2, Fig. 4), but exceeded previously reported values for the zone (Nugent et al. 1978, Tomasko & Lapointe 1991) (Table 2). Standing biomass and daily leaf production of *T. testudinum* were observed to vary greatly (>100-fold) over its distributional area (Table 2, Fig. 4), yet leaf turnover rates vary only about 5-fold (Table 2, Fig. 4). This suggests that differences in areal daily leaf production should be largely dependent on differences in standing biomass (Duarte 1989), rather than differences in productivity of individual shoots. This was confirmed by the fact that 88% of the variance in reported areal daily leaf production of *T. testudinum* productivity could be accounted for by differences in standing biomass (Fig. 4). Thus, *T. testudinum* standing biomass is the single most important factor accounting for differences in areal leaf production, as observed in Florida Bay by Zieman et al. (1989). Standing biomass appears, in turn, to be closely controlled by nutrient, particularly P, availability (Fourqurean et al. 1992). The suggestion that P availability may also control *T. testudinum* standing biomass in the Mexican Caribbean populations we examined is supported by the agreement between

Table 2. *Thalassia testudinum*. Biomass (g dry wt m^{-2}), productivity (g dry wt m^{-2} d^{-1}) and turnover (in % d^{-1} in parentheses) of different seagrass meadows. Values represent the range midpoint and average values for data reported as ranges or studies involving multiple stations, respectively. Control values reported when the work involved experimental manipulation of the seagrass bed. L: leaves, R: rhizome

Location	Plant part	Biomass	Production	Source
Cuba	L	517 ± 180	4.9 ± 0.44 (1.2 ± 0.18 % d^{-1})	Buesa (1974)
Barbados	L	1805	6.5 (1.4 % d^{-1})	Patriquin (1973)
	R		1.04	
Bermuda	L	4400	16.5	Patriquin (1973)
	R		2.02	
Florida (USA)	R	1552		Kenworthy & Thayer (1984)
Florida (USA)	L	65.2 ± 5.9	1.95 ± 0.12 (2.99 % d^{-1})	Zieman (1975)
Virgin Islands (USA)	L	207	1.4 (0.55 % d^{-1})	Williams (1987)
	R	1092		
Florida (USA)	L		(1.3 % d^{-1})	Barber & Behrens (1985)
Puerto Rico	L	450		Burkholder et al. (1959)
Florida (USA)	L	830		Jones (1968)
Florida (USA)	L		2.09 ± 0.41	Thorhaug & Roessler (1977)
Texas (USA)	L	373		Odum (1963)
Florida (USA)	L	700		Bauersfeld et al. (1969)
Veracruz (México)	L	353		Lot-Helgueras (1971)
Cuba	L	340		Buesa (1972)
Florida (USA)	L		5	Wood et al. (1969)
Florida (USA)	L	86.8 ± 2.7	1.84 ± 0.43 (2.01 % d^{-1})	Powell et al. (1989)
	R	793 ± 66		
Bahamas	L	200	3.23 (1.6 % d^{-1})	Capone et al. (1979)
Florida (USA)	L	46.7 ± 8.7	0.88 ± 0.22 (1.84 ± 0.35 % d^{-1})	Tomasko & Lapointe (1991)
Belize	L	43.2 ± 13.4	0.85 ± 0.18 (2.56 ± 0.11 % d^{-1})	Tomasko & Lapointe (1991)
Florida (USA)	L	49.5 ± 9.8	0.97 ± 0.19 (2.19 ± 0.12 % d^{-1})	Zieman et al. (1989)
Términos L. (México)	L	205 ± 28.7	6.57 ± 1.48 (3.2 % d^{-1})	Day et al. (1982)
	R			
Florida (USA)	L	905	4.55 (0.53 % d^{-1})	Bittaker & Iverson (1976)
	L	379 ± 157	6.38 ± 2.3 (1.8 ± 0.1 % d^{-1})	
Cancún (México)	R	345 ± 62	0.59 ± 0.15 (0.17 ± 0.02 % d^{-1})	This study

observed average standing crop (345 g dry wt m^{-2}, Table 2) and that predicted (249 ± 147 g dry wt m^{-2}) from the average leaf C: P ratio of their leaves (i.e. 618, Table 1) using the relationship between leaf C: P ratio and standing crop developed by Fourqurean et al. (1992) for Florida Bay.

The age structure of the populations (Fig. 3) allowed calculation of shoot recruitment and mortality rates (Table 1), and turnover rates of vertical rhizomes (Table 1), which were indicative, in turn, of those of horizontal rhizomes. These results demonstrated a close agreement between mortality and recruitment rates, as observed for *Cymodocea nodosa* in the past (Duarte & Sand-Jensen 1990a) and suggested the existence of interannual changes in shoot recruitment, consistent with the greater recruitment rates compared to mortality rates observed in the eutrophied lagoon (Table 1).

That shoots of *Thalassia testudinum* can be easily aged has been known for about 2 decades (Patriquin 1973, Durako & Moffler 1987, Cox & Tomlinson 1988),

yet, only recently has this technique been used to examine reproductive effort (Cox & Tomlinson 1988, Gallegos et al. 1992) and reconstruct interannual changes in leaf production and vertical growth (Marbà et al. unpubl.) of *T. testudinum* shoots. The results presented here add to these demonstrations of the great potential of aging techniques to reliably examine the dynamics of *T. testudinum* and other species (e.g. *Posidonia oceanica*, Pergent & Pergent-Martini (1990); *Cymodocea nodosa*, Duarte & Sand-Jensen (1990a, b)], and suggest that the path pointed out by Patriquin (1973) leads to a promising scientific journey. These methods provide convenient, although less accurate, alternatives to marking techniques (e.g. Zieman 1974) in areas where the recurrent visits required by marking techniques are difficult. These techniques should, therefore, help to expand our knowledge of seagrass dynamics to remote areas.
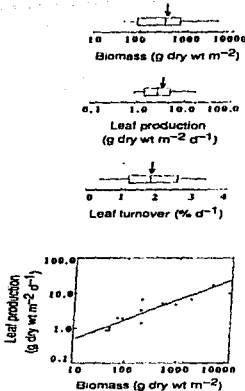
Fig. 4. *Thalassia testudinum*. Box plots summarizing available estimates of standing biomass, areal leaf production, and leaf turnover (from data in Table 2), and the relationship between standing biomass and areal leaf production. Boxes encompass the 25 to 75% quartiles of the data, lines extend to the 95% CL, and the vertical bar in each box indicates the position of the median value. Arrows on box plots indicate the average values encountered in this study (Table 2)

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Vertical growth of *Thalassia testudinum*: seasonal and interannual variability

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Abstract

The vertical growth of shoots of the seagrass *Thalassia testudinum* Banks ex König in four meadows, along a range of exposure to waves, in the Mexican Caribbean was examined to elucidate its magnitude and its relationship to sediment dynamics. Average internodal length varied between 0.17 and 12.75 mm, and was greatest in the meadow which experienced the greatest burial by sand waves moved by Hurricane Gilbert (September 1988). Internodal length showed annual cycles, confirmed by the flower scars always preceding or coinciding with the annual minimum internodal length. These annual cycles on the shoot allowed estimation of annual leaf production, which varied, on average, between 14.2 and 19.3 leaves per shoot year^{-1}. High vertical shoot growth was associated with long internodes and high leaf production rate, which increased with increasing vertical shoot growth to a maximum of approximately 25 leaves per shoot year^{-1}, with vertical growth of about 30 mm year^{-1} or more. Average internodal length showed substantial interannual differences from perturbations derived from the passage of Hurricane Gilbert. The growth response of the plants surviving moderate burial and erosion after the hurricane involved enhanced vertical growth and increased leaf production, and reduced vertical growth, respectively, after 1988. The variability in shoot vertical growth of *T. testudinum* can be separated into seasonal changes in plant growth, and long-term variability associated with episodic perturbations involving sediment redistribution by hurricanes.

Introduction

Seagrasses form extensive meadows over sandy, unstable sediments in shallow coastal areas (Den Hartog, 1970). Their response to sediment mobility involves, for most species, modified growth of their vertical shoots (i.e. short shoots), which raises the leaf-producing meristems nearer to the sediment surface (Den Hartog, 1973; Tomlinson, 1974; Marbà et al., 1993). Increased sediment deposition leads to enhanced vertical growth (Marbà et al., 1993)

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to relocate the leaf-producing meristems closer to the sediment surface, thereby minimizing leaf burial. Conversely, reduced sediment accretion rates or net erosion leads to reduced vertical growth to prevent the meristems from extending further above the sediment surface, and thus increasing the likelihood of physical damage. The net result of these responses is that variability in vertical growth is closely tuned to changes in sediment accretion (Tomlinson, 1974; Boudouresque et al., 1984; Marbà et al., 1993).

Growth of vertical shoots proceeds by the addition of internodes, the rhizome pieces between the insertion points of two consecutive leaves. Increased leaf production rate, which results in a greater number of leaves being produced annually by a shoot, should yield a parallel increase in the number of vertical internodes produced and, probably, in the annual vertical growth of the shoots. Moreover, the coupling between the growth of different seagrass modules (Duarte, 1991) suggests that productive shoots, which produce many leaves per year, may also develop large vertical internodes. Similarly, vertical internodes are expected to be longer during peak plant growth and smaller during periods of slow growth, as demonstrated for horizontal internodes of other seagrass species (e.g. Duarte and Sand-Jensen, 1990). Variability in the internodal length of seagrass vertical shoots must therefore reflect the combined effects of seasonal variability in plant growth, at seasonal time-scales, and altered sediment dynamics and changes in plant productivity at longer (interannual) time-scales.

Thalassia testudinum Banks ex König is the dominant seagrass in the Caribbean Sea, where it often experiences the consequences of altered sediment dynamics resulting from blow-outs (Patriquin, 1975) and hurricanes (Gallegos et al., 1993). Vertical growth must therefore be an important aspect of the ecology of *T. testudinum*. This contention is supported by recent findings that vertical growth of *T. testudinum* meadows in the Mexican Caribbean amounts to between 7.5 and 20 m of rhizome m^{-2} year^{-1}, and represents a considerable proportion of annual plant production (Gallegos et al., 1993). Circumstantial evidence supports the hypothesized relationship between sediment dynamics and *T. testudinum* vertical growth; Patriquin (1973) observed that plants exposed to high accretion rates had longer vertical internodes than those on more stable sediments.

In this study we examine the vertical growth of shoots of the seagrass *T. testudinum* in the Mexican Caribbean. We then quantify the importance of variability in the vertical elongation of its shoots at annual and interannual time-scales, and provide evidence that this reflects seagrass seasonality and plant response to disturbance by hurricanes and tropical storms, respectively.

Materials and methods

Vertical shoots (i.e. short shoots) were collected by divers in August 1991 and May 1992 from four meadows of *T. testudinum* growing across a range of

exposure to waves in the Mexican Caribbean, near Cancún (Fig. 1; see Gallegos et al., 1992, 1993 for additional details). The meadows examined ranged from fully exposed to the open sea (− 7 m in Bahía de Mujeres) to a meadow (− 2.5 m) next to a barrier reef subject to strong wave surges, a meadow next to the lagoon-reef beach (− 3 m) and a meadow growing in a protected coastal lagoon (Bojorquez lagoon; cf. Gallegos, 1993). In addition, we collected several old shoots from an erosional scarp near the beach (− 1.0 m) to examine vertical growth under erosional sediment regimes.

The time course of shoot vertical growth, represented by the sequence of internodal lengths (i.e. the distance between two consecutive leaf scars) along the vertical shoots, was measured under a dissecting microscope. The time unit of these sequences corresponds to the time interval involved in the formation of a vertical shoot internode, which equals the time interval between the initiation of two successive leaves on a shoot, and is referred to as plastochrone interval (Erickson and Michelini, 1957; Brouns, 1985a,b). Because time estimates based on plastochrone intervals are linearly related to those based on chronologic time, plastochrone intervals provide useful, indirect estimates of time (Erickson and Michelini, 1957; Brouns, 1985a,b). Flowering events along the life-span of the shoots examined were identified from the
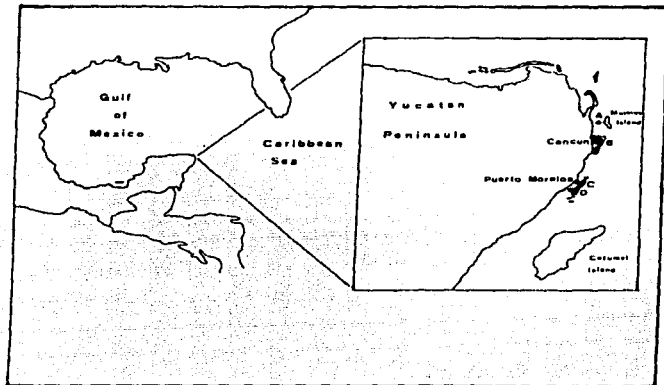

Fig. 1. Map of the study area showing the location of the meadows studied.

distinct scar left by the peduncle in the short shoots (Gallegos et al., 1992).
The sequences of vertical internodal lengths were smoothed (three- or five-
internode running average) to exclude short-term (less than 2 months) vari-
ability from the analysis.

Results and discussion

All populations examined, except for those growing at the erosional scarp,
showed some burial. The sediment depth at which living horizontal rhizomes
occurred was 5–10 cm in the coastal lagoon, 10–40 cm in the reef meadows,
and more than 70 cm in the meadow exposed to the open sea (Bahía de Mu-
jeres). Hurricane Gilbert (September 1988), the strongest hurricane hitting
the Mexican Caribbean this century (Fenner, 1991; Merino and Otero, 1991),
moved large sandwaves around Bahía de Mujeres (Aguayo et al., 1980). This
caused high mortality (C. Palillo, unpublished results, 1988) and burial of
the surviving shoots, which still had a third of the length of their leaves buried
below the sediment surface. Internodal length ranged widely (0.17–12.75
mm), varying significantly (one way analysis of variance (ANOVA),
$P < 0.0001$) among populations (Fig. 2), and was significantly longer in the
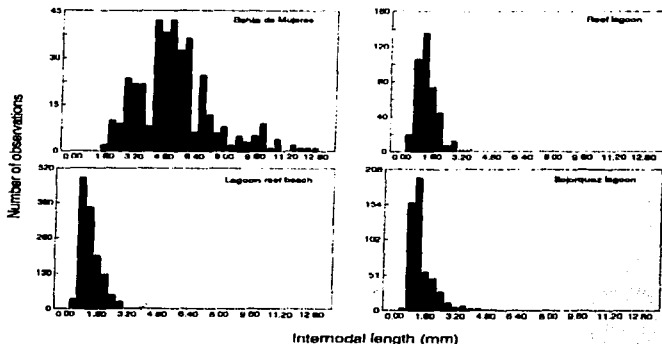open sea meadow at Bahía de Mujeres (Tukey multiple comparison test,

Fig. 2. Frequency distribution of vertical internodal lengths for *T. testudinum* shoots from the
different populations examined.

$P < 0.0001$), which also showed the greatest within-population variability (Fig. 2).

Examination of the time course of internodal length showed clear rhythmic cycles in vertical growth (Fig. 3). The number of internodes (which is equal to the number of leaves produced on a shoot) involved in these cycles (i.e. cycle period) was similar in magnitude to the annual leaf production for this species (about 20 leaves per shoot year^{-1}; Duarte, 1991). The annual nature of these cycles was confirmed by the fact that successive flowering events, which occur between March and May (Johnson and Williams, 1982; Gallegos et al., 1993), were separated by a single cycle (Fig. 3). Flowering always preceded or coincided with the annual minimum internodal length (Fig. 3), which indicated that minimal vertical growth (an indicator of a depression of seagrass growth) occurs some time in mid to late summer, whereas maximal growth rates occur in mid to late winter.

The presence of clear, annual cycles imprinted on the shoots allowed reconstruction of the annual leaf production (i.e. leaves per shoot year^{-1}) and vertical shoot growth, as previously shown for *Posidonia oceanica* (L.) Delile (Pergent and Pergent-Martini, 1990). These values showed the shoots of the
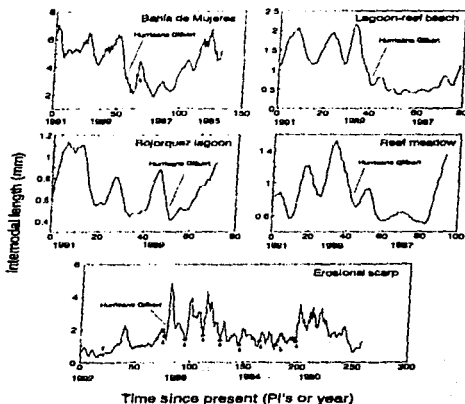

Fig. 3. Time sequence (in years and plastochrone intervals, PI) of changes in internodal length along *T. testudinum* shoots, where flowering events are recorded as arrows.

meadow growing at the reef-lagoon beach to produce the fewest leaves (mean, 14.2 leaves per shoot $year^{-1}$; Fig. 4), and those exposed to the open sea (Bahía de Mujeres) to have the largest vertical shoot growth, consistent with the larger burial observed there, and to produce more leaves (19.3 leaves per shoot $year^{-1}$) than the shoots in the other meadows (Fig. 4).

Annual vertical shoot growth is the product of the number of leaves (internodes) produced and the average length of the internodes. Hence annual vertical growth may vary because of changes in the number of leaves produced per year and/or changes in internodal length. High vertical shoot growth was associated with high leaf production rate and long internodes ($r = 0.71$ and 0.91, respectively; Fig. 5). Further examination of these relationships indicates that average internodal length increases along the range of vertical shoot growth encountered (Fig. 5), whereas increased leaf production is associated
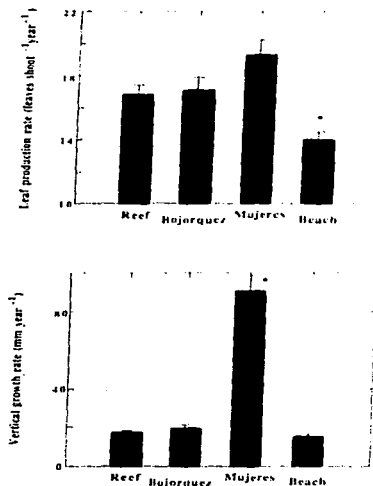

Fig. 4. Average (+ S.E.) leaf production and vertical growth rate for the *T. testudinum* populations studied. *, average values significantly different (*t*-test, $P < 0.05$) from the rest.
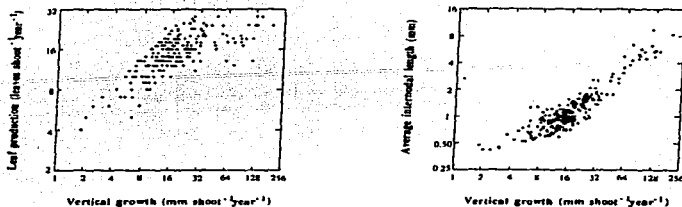
Fig. 5. The relationship between the annual vertical growth and leaf production and average internodal length for the *T. testudinum* populations examined.

with increased vertical shoot growth up to about 30 mm year^{-1} (Fig. 5). The asymptotic leaf production observed at high vertical shoot growth (about 25 leaves per shoot year^{-1}; Fig. 5) is close to the average leaf production for *T. testudinum* populations (23.3 leaves per shoot year^{-1}; Duarte, 1991), and may therefore represent the upper limit to its leaf production in this area.

The sequences of internodal lengths of the oldest shoots sampled reveal, in addition to the presence of annual cycles, the existence of substantial (up to five-fold) interannual differences in average internodal length (Fig. 3). Most shoots examined showed modified interannual average vertical growth around 1988 (Fig. 3), the year of passage of Hurricane Gilbert. The hurricane displaced large volumes of sediments, causing substantial burial in some places (e.g. Bahía de Mujeres) and erosion in some others (e.g. erosional scarp in the reef-lagoon beach). The growth response of the plants surviving burial involved enhanced vertical growth and increased leaf production after 1988 (Fig. 3). Conversely, the shoots collected at the erosional scarp showed reduced vertical growth after 1988 (Fig. 3).

The increased vertical shoot growth following burial (e.g. Bahía de Mujeres, Fig. 3) and the reduced vertical growth following erosion (e.g. erosional scarp, Fig. 3) support the association between vertical shoot growth and sediment dynamics reported for seagrasses elsewhere (Patriquin, 1973; Boudouresque et al., 1984; Marbà et al., 1993). Our results also support the idea that growth of the various plant parts takes place in a coordinated way, by demonstrating a relationship between vertical shoot growth and leaf production rate (Fig. 5). It has been shown that moderately increased sediment accretion may stimulate seagrass growth experimentally for *Cymodocea nodosa* (Ucria) Aschers. (Marbà and Duarte, 1993). This has also been suggested for *P. oceanica* in the past (Boudouresque et al., 1984), and this is also consistent with reports that burial stimulates growth of dune (e.g. *Ammophila*

breviligulata Fern.; Disraeli, 1984; Maun and Lapierre, 1984) and marsh (Pezeshki et al., 1992) plants. The relationship between burial and enhanced growth of surviving plants is, presumably, not linear, for plants should experience increased mortality as burial increases to reach an upper limit where complete mortality occurs (Marbà and Duarte, 1993).

Long-term changes in vertical growth were particularly obvious for the oldest shoot we collected (Fig. 6). It had lived for about 18 years (260 plastochrone intervals) and produced nine flowers during that time, far exceeding the maximum life span of 9.5 years (Gallegos et al., 1993) and maximum

Time since present (P.I. and years)

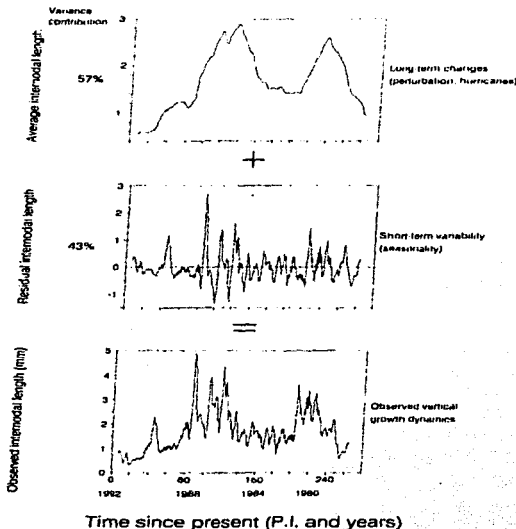Fig. 6. The partitioning of the observed time sequence of vertical growth for the oldest *T. testudinum* shoot collected into an interannual component (calculated by smoothing the data with a filter equivalent to 2 years), and a seasonal component (i.e. the difference between the interannual component and the observed sequence). Variance proportions accounted for each of these time-scales were calculated using nested ANOVA.

flower production of four flowers (Gallegos et al., 1992) observed for *T. testudinum* shoots in the past. The changes observed involved vertical growth minima around 1982–1984 and 1988–1989 (i.e. about 70 and 170 plastochrone intervals from May 1992, Fig. 6), probably responding to erosion events similar to those caused by Hurricane Gilbert in 1988, separated by periods of comparatively high vertical shoot growth, indicative of sediment replenishment at the erosional scarp. This pattern suggests that long-term disturbances of vertical shoot growth may show some periodicity (about 7–8 years period; Fig. 6). Hurricanes (depressions with associated wind velocities > 28 m s^{-1}) are the major vectors of sediment redistribution in the Mexican Caribbean, where they occur with a frequency of about 5–6 years (Merino and Otero, 1991). Thus, hurricanes should be the main agents of the large interannual changes observed in the vertical growth of turtlegrass in the Mexican Caribbean (Figs. 3 and 6). In addition to this effect, moderate burial following hurricanes also appears to result in greater flowering intensity (Gallegos et al., 1992), consistent with reports of increased flowering intensity with increasing burial of dune plants (Eldred and Maun, 1982). Because of the low frequency of these perturbations (about 7–8 years) compared with the average life-span of *T. testudinum* shoots (1.5 years; Gallegos et al., 1993), long-term perturbations, such as those induced by hurricanes, are likely to occur only once during their life-span, and be traced as unique events, rather than cycles in their vertical shoot growth.

The variability in vertical shoot growth of *T. testudinum* can thus be separated into a short-term component (annual — 43% of the variability in the oldest shoot here), associated with seasonal changes in plant growth, and a long-term component (interannual — 57% of the variability in the oldest shoot here), associated with episodic perturbations involving sediment redistribution by hurricanes (Fig. 6). The vertical growth of *T. testudinum* shoots is, therefore, not only an important adaptative component of seagrass survival in mobile sandy sediments, but also a record of past seasonality and, in old shoots, perturbation history (Fig. 6). Evaluation of *T. testudinum* vertical growth therefore holds great potential to reconstruct past-growth dynamics, similar to that contained in the scale thickness of the seagrass *P. oceanica* (Pergent and Pergent-Martini, 1990), the vertical growth of *C. nodosa* (Marbà et al., 1992) and the width of tree rings.

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EVIEW

Reconstruction of seagrass dynamics: age determinations and associated tools for the seagrass ecologist

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ABSTRACT: All seagrasses are rhizomatous plants that grow by reiteration of a limited set of modules. Their past growth history can therefore be reconstructed from the scars left by abscised leaves and flowers on the long-lived rhizomes of the seasonal signals imprinted in the frequency and size of their modules. We provide here the basic foundations and assumptions of these reconstruction techniques and the calculations involved in their application. We then show their reliability and potential to quantify an array of ecological processes, such as plant demography, leaf and rhizome production, flowering intensity, and seagrass responses to anthropogenic perturbations based on our recent studies of Mediterranean, Caribbean and Indo-Pacific seagrass species. Reconstruction techniques have also proven useful in demonstrating the role of seagrasses as tracers of sediment movement over seagrass beds and the rates of colonisation and expansion of seagrass patches. These reconstruction techniques should provide a powerful tool to improve our knowledge of seagrass species and populations from remote areas based on a single or just a few visits. This should, therefore, allow us to sample many seagrass meadows using limited resources, thus generating a strong foundation for the study of comparative seagrass ecology and testing of theories previously applied to terrestrial plant populations.

KEY WORDS: Seagrasses · Age determinations · Growth · Demography · Dynamics

INTRODUCTION

tnalisation of the key role of seagrasses in coastal >systems has fostered ever-growing efforts to quan-
' their annual productivity and growth dynamics.
o geographic distribution of this effort has been,
wever, concentrated in regions in the USA,
ribbean Basin and Bahamas, western Europe, Aus-

tralia and the western Mediterranean, with only a few studies focused on seagrasses elsewhere. This patchy distribution of research effort is largely attributable to the need for repeated sampling to determine seagrass growth, which is the main constraint to extending our knowledge to regions away from research laboratories. A better geographical balance of our knowledge of seagrass ecology is needed to ensure that this knowl-

edge refers to the general case, rather than the exceptions, and to allow reliable calculations of the role of seagrasses in the dynamics of the global and coastal ocean. Hence, our knowledge of seagrass ecology and their responses to perturbations would become more general and relevant if techniques were available that allowed the quantification of seagrass growth dynamics from one or a few visits (Gallegos et al. 1993). These techniques are available, but their full potential has yet to be developed.

Petersen (1913) was the first to use the sequence of rhizome internodal lengths of the seagrass *Zostera marina* to calculate productivity in Danish waters. Over half a century later, Patriquin (1973) outlined the basic ideas and demonstrated how measurements based on age determinations could help to study the growth of *Thalassia testudinum*. These techniques have as a common basis the ability to determine the age of seagrass rhizomes (e.g. Petersen 1913, Patriquin 1973, Duarte & Sand-Jensen 1990a, b, Gallegos et al. 1993). Techniques based on age determinations have been used since, alone or in combination with standard marking techniques, to reconstruct different aspects of seagrass ecology (Table 1). Yet, these techniques have been applied only to a limited number of genera (Table 1), leading to the misconception that they are species-specific. As a consequence, their applicability to a wider set of seagrass species remains untested and their potential unexplored. Techniques based on age determinations can be applied, however, to study the growth of most seagrass flora, and the generality of these techniques is best suggested by the fact that

essentially the same techniques have been used to study growth and demography of a range of plants (e.g. Sarukán 1978, Duke & Pinzón 1992).

Our goal here is to formalise the use of techniques based on age determinations as powerful tools to reconstruct seagrass dynamics from a single or a few sampling event(s), and therefore encourage their use to expand the geographic spread of our knowledge of seagrass ecology. We do this by describing the basic foundations and assumptions of the methods and the calculations involved in their application. We then describe the applicability of the methods to different seagrass species, using data from Mediterranean, Caribbean and Indo-Pacific species.

TECHNIQUES BASED ON AGE DETERMINATIONS AND PLASTOCHRONE INTERVALS

The foundation of reconstruction methods

The set of reconstruction techniques described here take advantage of the simple architecture of seagrasses described by den Hartog (1970) and more explicitly by Tomlinson (1974). Seagrasses are rhizomatous plants that grow by reiteration of a limited set of modules (Fig. 1). These are (1) rhizome internodes, which ensure the vegetative spread of the organism and may be horizontal (also referred to as long shoots) or erect (also referred to as short or vertical shoots), depending on whether they spread the plant sidewards or upwards, (2) leaves, where photo-

Table 1. A compilation of the use of techniques based on age determinations to examine different aspects of seagrass ecology

Aspect studied	Species	Source
Shoot demography	*Cymodocea nodosa*	Duarte & Sand-Jensen (1990a, b), Perez et al (1994)
	Halodule wrightii	Gallegos et al (1994)
	Syringodium filiforme	Gallegos et al (1994)
	Thalassia testudinum	Gallegos et al (1993)
Leaf production	*Zostera marina*	Petersen (1913), Sand-Jensen (1975)
	Cymodocea nodosa	Duarte & Sand-Jensen (1990a, b)
	Posidonia oceanica	Pergent & Pergent-Martini (1990)
	Halodule wrightii	Gallegos et al. (1994)
	Syringodium filiforme	Gallegos et al. (1994)
	Thalassia testudinum	Patriquin (1973), Gallegos et al. (1993)
Rhizome growth	*Cymodocea nodosa*	Perez (1989), Duarte & Sand-Jensen (1990a, b), Terrados & Ros (1992)
	Posidonia oceanica	Pergent & Pergent-Martini (1990)
	Halodule wrightii	Gallegos et al. (1994)
	Syringodium filiforme	Gallegos et al. (1994)
	Thalassia testudinum	Patriquin (1973, 1975), Gallegos et al. (1993)
Flowering intensity	*Cymodocea nodosa*	Gallegos (unpubl.)
	Posidonia oceanica	Pergent & Pergent-Martini (1990)
	Thalassia testudinum	Durako & Moffler (1987), Cox & Tomlinson (1988), Gallegos et al. (1992)
Colonization rate	*Cymodocea nodosa*	Duarte & Sand-Jensen (1990a, b)

synthesis and nutrient uptake from the water column occur, and which arise from growing meristems at the rhizome apices; and (3) roots, which serve to anchor the plant and take up sediment nutrients, and appear at regular intervals along the rhizome. The insertion points of the leaves on the rhizome are referred to as nodes and are identifiable by the scars left after leaf abscission (Fig. 1). Accordingly, the rhizome pieces in between 2 consecutive leaf scars are termed rhizome internodes. These are produced in the time interval between the formation of 2 successive leaves, which is termed plastochrone interval (Erikson & Michelini ·1957). This architecture ensures a close (1–1) relationship between the production of rhizome internodes and leaves.

This simple depiction of seagrass growth becomes more complex as the degree of differentiation between vertical and horizontal rhizomes increases (cf. Tomlinson 1974), from species with monomorphic rhizomes (e.g. genera *Zostera* and *Enhalus*) to those with differentiated major (long shoots) and minor (short shoots) axes (e.g. genera *Thalassia*, *Thalassodendron* and *Cymodocea*; Fig. 2). Increasing differentiation between vertical and horizontal rhizomes is associated with greater differences in the size and rhythm of formation of leaves and rhizome internodes on the 2 axes. Verti-

cal rhizomes usually have longer leaves, shorter internodes, and longer plastochrone intervals than horizontal rhizomes (Duarte 1991). The leaves produced by the horizontal meristem of *Thalassia* sp., which represent an advanced differentiation between horizontal and vertical rhizomes, are reduced to small bracteae (Tomlinson & Vargo 1966). Lateral branches have also been reported to grow slower and have shorter internodes than primary axes (Brouns 1987). The faster growth rates of primary axes compared to branches, whether lateral or vertical (i.e. shoots), are probably a consequence of the strong apical dominance typical of rhizomatous plants (Bell & Tomlinson 1980).

The close (1 : 1) relationship between the production of rhizome internodes and leaves is the basis for age determinations of seagrass shoots and rhizomes, which can be estimated as the number of leaf scars (or internodes) plus standing leaves produced since the appearance of the shoot or rhizome of interest. The basic time units of the resulting age estimates are plastochrone intervals, which have been proposed to represent the internal growth rhythm of the plants, thereby providing useful estimates of 'biological time' (Erickson & Michelini 1957, Lamoreaux et al. 1978). Yet, these time units are species-specific (cf. Duarte 1991) and also depend on environmental conditions (e.g. Hillman et al. 1989) and are, therefore, difficult to compare among different species or to integrate into ecosystem models, which require their translation into absolute time (e.g. days) to express rates (cf. Duarte 1991).

Translating plastochrone intervals into absolute time units

The translation of plastochrone intervals into absolute time assumes linearity between the 2 time units (Erickson & Michelini 1957, Patriquin 1973). The annual mean duration in days of a plastochrone interval (PI) is to a large extent a species characteristic. This is reflected in the much greater variance between than within species (coefficient of variation 139 % and 17 % respectively; Duarte 1991), which depends on environmental conditions (e.g. Hillman et al. 1989). The annual average mean plastochrone intervals for different species range between 1.1 and 47.2 d PI^{-1} for vertical rhizome internodes and associated leaves, and between 1.7 and 42.4 d PI^{-1} for horizontal rhizome internodes and associated leaves (Duarte 1991). Thus, annual means of species-

Fig. 1. Modules of a typical seagrass

Fig. 2. Gradient of increasing differentiation between horizontal and vertical rhizomes in different seagrass genera, from those with no differentiation to those which only have leaves on the vertical rhizomes

specific plastochrone intervals may be used as a first approximation to translate PI into absolute time. Yet, there is considerable variability in PI within species, resulting from environmental differences, reflected both in differences among populations and variability at interannual and seasonal time scales within populations. Consequently, reliable estimates of seagrass age should be based on population-specific estimates of PI duration in days.

The annual mean PI may be remarkably constant for some species (e.g. 26 to 33 d for *Cymodocea nodosa*, Caye & Meinesz 1985, Perez 1989, Duarte & Sand-Jensen 1990a). Terrados & Ros 1992), and vary substantially among populations of other species (e.g. 28 to 69 d in *Posidonia oceanica*, T. Alcoverro unpubl.). Differences in the annual mean PI among populations are likely to derive from differences in the growth conditions they experience. Hence, the rhythm of leaf formation has been shown to depend on light availability (e.g. Hillman et al. 1989), temperature (Barber & Behrens 1985), nutrient availability (Short 1987, Perez et al. 1991), and sediment dynamics (Gallegos et al. 1993). Interannual differences in leaf PI occur (e.g. Pergent & Pergent-Martini 1990, Marbà et al. 1994a) associated with interannual differences in growth conditions (light, nutrients, etc.) and perturbations, such as altered sediment dynamics

(Marbà et al. 1994a). Interannual variability in PI is usually much smaller than seasonal variability, such that the linearity between PI and absolute time assumed by these age determinations is best supported at interannual time scales (cf. Brouns 1985a, b). Estimates of seagrass age are, therefore, more accurate for long-lived (>1 yr) than for short-lived seagrass species (cf. Duarte 1991). This explains why techniques based on age determinations have mostly been applied in the past to seagrasses living longer than 1 yr (Table 1)

Seasonal variation in PI is considerable in the temperate zone, where leaf production is reduced during winter (e.g. Sand-Jensen 1975, Perez 1989, Terrados & Ros 1992). Yet, tropical seagrasses also display some, at times considerable, seasonality in leaf formation rate (Brouns 1985b) which is difficult to attribute to limiting light or temperature. This variability may be triggered instead by intrinsic phenologic events, such as flowering and reproduction, with the associated drainage of resources. The clues for the seasonal pattern of tropical seagrasses may be annual changes in photoperiod, as has been reported for tropical plants on land (Duke & Pinzon 1992). Indeed, growth minima of *Thalassia testudinum* in the Mexican Caribbean, where incoming irradiance and water temperature are permanently high (van Tussenbroek 1993), follow flowering (Galle-

gos et al. 1992, Marbá et al. 1994a). Seasonal variabil-
ity in PI must be smaller in slow-growing seagrasses,
which integrate seasonal variability better in their long
PI (Duarte 1991).

Direct measurements of the plastochrone interval

Direct measurements of the duration of leaf PI
(d leaf $^{-1}$) are obtained from observations of the emer-
gence of new, unmarked, leaves on marked shoots
(Zieman 1974).

$$PI = \frac{\text{Time interval (d)} \times \text{No. of marked shoots}}{\text{No. of leaves formed on marked shoots}}$$

Leaf PI is usually measured over short periods (e.g.
9 to 30 d; e.g. Brouns 1985a), when shoots have pro-
duced at most a single leaf. The basic data obtained for
each shoot are, therefore, binary (0 or 1 new leaf
formed), and the estimated PI represents the inverse of
the fraction of shoots that formed new leaves over the
marking period. Statistical tables indicate that the
error around fractions is considerable at small sample
sizes (Sokal & Rohlf 1981). For instance, 100 marked
shoots are required to obtain a 95 % confidence limit of
10 % of the mean proportion of shoots that developed
new leaves when only half of the shoots did so. Hence,
a large number of shoots must be marked to obtain
reasonably precise estimates of plastochrone interval
duration for measurement periods shorter than the
expected plastochrone intervals (Brouns 1985a). Alter-
natively, more precise PI estimates are obtained when
marking periods are extended to have more than 1 leaf
produced, on average, on each shoot (Brouns 1985a).
This, however, reduces the temporal resolution of the
sampling programme and increases the risk of losing
marked leaves, thereby underestimating leaf growth.

Reconstruction techniques to estimate plastochrone intervals

Direct measurements of seagrass plastochrone inter-
vals require repeated sampling and considerable sam-
pling effort, such that researchers using marking tech-
niques often choose to base their estimates of seagrass
growth on the observed leaf extension instead of using
techniques based on age determinations. The use of
techniques based on age determinations, however, is
more convenient when the PI is already known. Addi-
tionally, PI can be estimated from seasonal signals
imprinted in the size of seagrass modules (e.g. Duarte
& Sand-Jensen 1990b, Pergent & Pergent-Martini
1990, Gallegos et al. 1993), much like the marks used
to estimate annual growth of molluscs, fish and trees.

The seasonality of seagrass growth results in annual
cycles in the size of leaves, petioles, and rhizome
internodes (Duarte & Sand-Jensen 1990b, Pergent &
Pergent-Martini 1990, Gallegos et al. 1993). Time
series of module size allow, therefore, the inference of
the number of modules produced annually. The 1:1
correspondence between rhizome internodes and
leaves implies that knowledge of the number of rhi-
zome internodes produced per year can be easily
translated into the number of leaves and the annual
mean PI.

Because leaf longevity is generally < 1 yr (Duarte
1991), leaves representing consecutive annual length
maxima or minima are not alive on any one shoot. Sea-
sonal cycles in leaf size are, therefore, useless to recon-
struct the annual mean PI, and only modules remain-
ing in the plant for more than 1 yr, allowing the
presence of modules produced during consecutive
growth maxima (or minima) at any one time, can be
used to infer the annual mean PI. The petioles or
sheaths of the leaves of some seagrasses (e.g. *Thalassia
testudinum*, *Posidonia oceanica*, *Enhalus acoroides*)
remain attached to the shoots long after the leaves are
shed. The thickness of *P. oceanica* petioles or sheaths
has been shown to exhibit annual cycles (Pergent &
Pergent-Martini 1990). Whether the thickness of
standing petioles of other species shows similar annual
cycles has, however, not been tested.

Seagrass rhizomes live longer than leaves (Duarte
1991), and some rhizomes live for decades (e.g.
Cymodocea nodosa, Duarte & Sand-Jensen 1990a,
Thalassia testudinum, Marba et al. 1994a). This
longevity renders seagrass rhizomes the most appro-
priate tool to reconstruct the annual mean duration of
PI. Moreover, cycles in a variable can only be unam-
biguously identified in series at least 3-fold longer than
the expected period. Thus, use of the time series of rhi-
zome internodal length to reconstruct the annual mean
PI is most precise for seagrasses whose rhizome lives
for more than 3 yr.

The use of annual cycles in the length of rhizome
internodes found in many seagrass species to estimate
PI, and subsequently leaf productivity, was first noted
in *Zostera marina* by Petersen (1913). This strong sea-
sonality was later demonstrated in the Mediterranean
species *Cymodocea nodosa* (Cayé & Meinesz 1985,
Duarte & Sand-Jensen 1990b), allowing estimates of
annual mean PI similar to those obtained using direct
measurements (Duarte & Sand-Jensen 1990b). How-
ever, reconstruction of annual mean PI from horizontal
rhizomes requires the examination of intact rhizomes
pieces produced over more than 1 yr. It requires, in the
case of *Cymodocea nodosa*, rhizome pieces more than
1 m long (Duarte & Sand-Jensen 1990a, Duarte 1991).
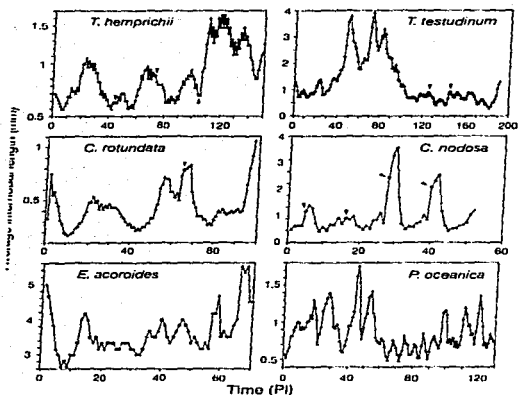Hence, even though horizontal rhizomes are often suf-

Fig. 3. Time series of vertical internodal length for different seagrasses sampled in the South China Sea, the Philippines (*Thalassia hemprichii*, *Cymodocea rotundata* and *Enhalus acoroides*; Fortes unpubl.), the Mexican Caribbean (*Thalassia testudinum*; Gallegos unpubl.), and the Spanish Mediterranean (*Posidonia oceanica* and *Cymodocea nodosa*; Duarte unpubl.). The time series show annual cycles in vertical growth which can be used to infer the number of internodes (= number of leaves) produced per shoot per year. Arrowheads indicate the position of successive flowering events along the shoot. Pl: plastochrone intervals

ciently long-lived to be used for estimation of mean annual Pl, the long rhizome pieces required may be difficult to retrieve.

We recently described the presence of seasonal patterns imprinted in the sequence of vertical internodal length of *Thalassia testudinum* shoots (Gallegos et al 1992, Marbà et al. 1994a), which are easy to sample in comparison with horizontal rhizomes. This finding moved us to examine the sequence of internodal lengths of shoots of many other seagrasses, which consistently revealed similar seasonal signals (Fig. 3). These findings have a precedent in the study of tropical trees, for annual periodicity in internodal length has been described for other plants, such as mangroves (uke & Pinzón 1992).

Vertical rhizome growth also responds strongly to changes in sediment dynamics (e.g. Patriquin 1973, Budouresque et al. 1984, Gallegos et al. 1993, Marbà et al. 1994a, b), which may disturb the annual signal in the series of vertical internodal length. Identification annual cycles in internodal length in these cases

requires that short-term and interannual variability be filtered out to highlight the seasonal signal. This can be achieved by applying a high- and low-frequency (e.g. running averages of ca 30 and ca 150% of the expected number of internodes contained in a cycle, respectively) filter to the raw data, which yields clearer signal at the seasonal scale (Fig. 4).

The considerable seasonality of rhizome growth in some seagrasses implies that the rate of production of new short shoots, which appear at regular intervals along the rhizomes, should be similarly seasonal. This conclusion is supported by many reports of seagrass seasonality which demonstrate shoot recruitment (i.e. density increase) to occur mostly in spring (e.g. *Cymodocea nodosa*, Terrados & Ros 1992; *Zostera marina*, Sand-Jensen 1975; *Heterozostera tasmanica*, Bulthuis & Woelkerling 1981). Hence, shoots appear in cohorts, rather than continuously throughout the year. This is reflected in the presence of distinct modes in frequency distributions of shoot age, given a sufficiently large (i.e. ca 1000) sample size (e.g.
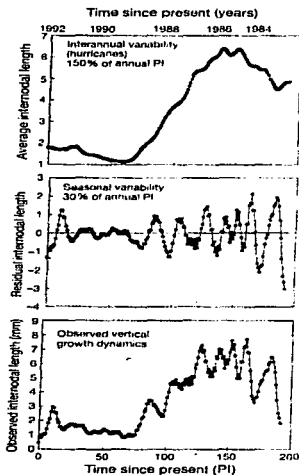
Fig. 4. *Thalassia testudinum* Separation of the time series of vertical internodal length of samples from the Mexican Caribbean (Gallegos unpubl.) into a long-term (interannual) and a seasonal component. The long term component was obtained applying a filter (i.e. running average) equal to 150% of the number of internodes produced annually [17], and the seasonal component was obtained by subtracting the long-term component from the time series, which was then filtered for short-term variability (i.e. running average of 5 internodes or about 30% of the annual number of leaves produced per year). PI: plastochrone intervals

Cymodocea nodosa, Duarte & Sand-Jensen 1990b; Fig. 5). The presence of these cohorts allows the calculation of the number of leaves produced per shoot per year as the mean age difference between cohort modes (Fig. 5).
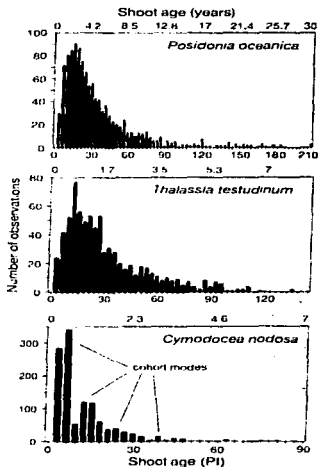

Fig. 5. Age frequency distribution (in plastochrone intervals [PI] and years) of living short shoots of different seagrasses sampled in the Spanish Mediterranean (*Posidonia oceanica* and *Cymodocea nodosa*, Duarte unpubl.) and the Mexican Caribbean (*Thalassia testudinum*, Gallegos et al. 1993)

The annual mean PI can also be identified from flowering marks in species with a single flowering period per year (e.g. *Cymodocea* sp., *Thalassia* sp.). This is possible when flowering produces an identifiable scar on the shoot, whether scars left by the flower peduncle (e.g. the genus *Thalassia*, Cox & Tomlinson 1988, Gallegos et al. 1992; the genus *Cymodocea*, Marbà unpubl.; Fig. 3) or other marks, such as the peculiar flower stalks of *Posidonia oceanica* (Pergent et al. 1989). Even though flower peduncles may not be formed in a synchronous manner over a short time
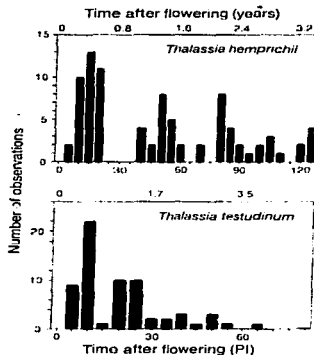
Fig. 6. Distribution of time elapsed (as plastochrone intervals (PI) units and years) since different short shoots flowered in populations sampled in the Mexican Caribbean (*Thalassia testudinum*, Gallegos et al. 1992) and the South China Sea, the Philippines (*Thalassia hemprichii*, Fortes unpubl.)

period (cf. Durako & Moffler 1987), the distribution of time elapsed since flowering (as PI) shows distinct modes identifying the period of peak flowering (e.g. fall for *P. oceanica*, March–May for *T. testudinum* in the Mexican Caribbean; and May–June for *C. nodosa* in the Mediterranean) in successive years (Fig. 6). The time difference between these flowering modes corresponds to 1 yr or multiples of this time (Fig. 6), thereby allowing the estimation of the number of plastochrone intervals in 1 yr as the minimum common multiple of these modes. Estimates based on the identification of flowering marks show good agreement with independent estimates (e.g. Gallegos et al. 1992), but may overestimate the PI for species which shoots reduce or stop leaf production during flowering (M. J. Durako pers. comm.). Because of the low fraction of shoots flowering each year (about 10% on average for different seagrass species; Gallegos et al. 1992) many shoots need be collected to ensure adequate estimation of plastochrone intervals in this way.

Reconstruction of the plastochrone interval using age determinations is subject to different sources of uncertainty. It is, therefore, recommended that several of these methods be used simultaneously to cross-validate the estimates obtained. Available results, however, demonstrate that the estimates of annual mean leaf production per shoot obtained using reconstruction techniques are strongly correlated to the observed (using marking techniques) annual leaf production (no. of leaves shoot^{-1} yr^{-1}).

$$\text{Observed} = 2.5 \, (\pm 0.75) + 0.85 \, (\pm 0.06) \, \text{Reconstructed} \\ (R^2 = 0.96, \, p < 0.0001)$$

although there is a weak tendency for reconstructed values to be somewhat lower than those derived from marking techniques for species producing a small number of leaves per shoot annually (Fig. 7). Annual mean leaf production per shoot estimated using reconstruction techniques was not significantly different from estimates obtained using marking techniques (mean difference between observed and reconstructed 0.22 ± 0.54, $p = 0.69$, Fig. 7), thereby demonstrating the potential and validity of reconstruction techniques.

Reconstructing seagrass dynamics: the tool box

Seagrass growth

Reconstruction techniques allow calculation of the rate of production of different seagrass modules. This information allows the application of demographic growth analysis, which yields growth estimates remarkably close to those obtained using traditional growth analysis based on mass produced (e.g. Sand-Jensen 1975, McGraw & Garbutt 1990a, b). Hence, the set of reconstruction techniques described here hold great potential as alternative methods to estimate seagrass production (Patriquin 1973, Pergent & Pergent-Martini 1990, Gallegos et al. 1993).

The descriptor of seagrass growth which can be most readily obtained using reconstruction techniques is the average number of leaves produced annually per shoot. All the reconstruction methods to estimate the mean annual PI described above enable the calculation of the number of leaves produced per shoot (i.e. 365/PI). This can be used as a surrogate of seagrass growth, therefore enabling one to examine interannual variability in seagrass growth. Using this technique Pergent (1990) identified a 3 to 6 yr cycle and an 11 yr cycle in the growth of *Posidonia oceanica*. Marbà et al. (1994a) described increased growth of *Thalassia testudinum* buried <70 cm by sand by the passage of Hurricane Gilbert in the Mexican Caribbean; and
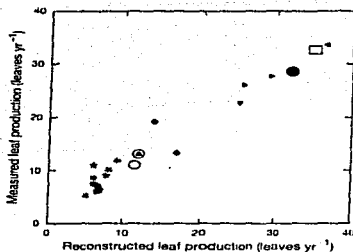
Fig. 7. Relationship between the number of leaves produced annually, estimated using marking and reconstruction techniques, for different seagrass species sampled in the Spanish Mediterranean (● *Posidonia oceanica*, ▼ *Zostera marina*, ▼ *Zostera noltii*, ○ *Cymodocea nodosa*), the Caribbean Sea off Yucatán Peninsula, Mexico (● *Thalassia testudinum*, ✴ *Syringodium filiforme*, Gallegos unpubl.) and the South China Sea, the Philippines (◄ *Thalassia hemprichii*, ● *Cymodocea rotundata*, □ *Cymodocea serrulata*, ▲ *Enhalus acoroides*, Fortes unpubl.)

Fortes (unpubl.) identified a correlation between growth of *Enhalus acoroides* and interannual weather patterns. This technique may prove particularly useful to study the consequences of perturbations to seagrass populations for which no background data exist. In addition, estimates of the average number of leaves annually produced per shoot allow calculation of the average annual leaf turnover and leaf production. Annual leaf turnover can be calculated as the ratio between the number of leaves produced per year and the average number of standing leaves per shoot, and annual shoot leaf production as the product of the number of leaves annually produced per shoot and the mean weight of fully developed leaves.

More important, these techniques also enable reconstruction of rhizome growth (Patriquin 1973, 1975, Duarte & Sand-Jensen 1990a, Pergent & Pergent-Martini 1990, Terrados & Ros 1992, Gallegos et al. 1993) Patriquin (1973) noted that the growth rate of the rhizome may be obtained by dividing the length of the rhizome between 2 shoots by the difference in the ages of the 2 shoots. This simple ratio is, however, appropriate only for species producing new shoots along the rhizome at time intervals longer than 1 leaf PI, so that con-

Fig. 8. Relationship between the number of rhizome internodes in between shoots connected along rhizome chains and sampled in the Spanish Mediterranean (*Cymodocea nodosa*, Duarte unpubl.) and the South China Sea, the Philippines (*Cymodocea rotundata*, Fortes unpubl.) and their age differences. The slopes of these relationships indicate the average number of internodes produced per plastochrone interval (PI) and allow, in combination with the average internodal length, calculation of rhizome elongation rate

secutive shoots differ in age by > 1 leaf PI. An alternative, more accurate, way to calculate rhizome elongation rate is to regress the number of internodes in between 2 shoots connected along a rhizome piece against their age difference (Fig. 8). The regression slope represents

Fig. 7. Relationship between the number of leaves produced annually, estimated using marking and reconstruction techniques, for different seagrass species sampled in the Spanish Mediterranean (● *Posidonia oceanica*, ▶ *Zostera marina*, ▼ *Zostera noltii*, ○ *Cymodocea nodosa*, Martin unpubl.), the Caribbean Sea off Yucatan Peninsula, Mexico (◆ *Thalassia testudinum*, ✦ *Syringodium filiforme*, Gallegos unpubl.) and the South China Sea, the Philippines (◀ *Thalassia hemprichii*, ● *Cymodocea rotundata*, □ *Cymodocea serrulata*, ▲ *Enhalus acoroides*, Fortes unpubl.)

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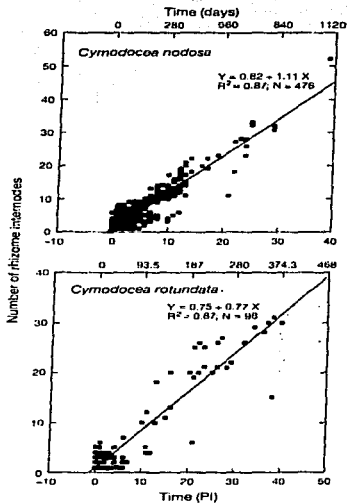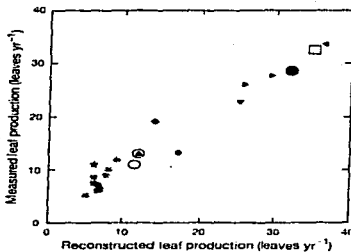

Fig. 8. Relationship between the number of rhizome internodes in between shoots connected along rhizome chains and sampled in the Spanish Mediterranean (*Cymodocea nodosa*, Duarte unpubl.) and the South China Sea, the Philippines (*Cymodocea rotundata*, Fortes unpubl.) and their age differences. The slopes of these relationships indicate the average number of internodes produced per plastochrone interval (PI) and allow, in combination with the average internodal length, calculation of rhizome elongation rate

secutive shoots differ in age by > 1 leaf PI. An alternative, more accurate, way to calculate rhizome elongation rate is to regress the number of internodes in between 2 shoots connected along a rhizome piece against their age difference (Fig. 8). The regression slope represents

Fig. 9. Relationship between the length of vertical shoots of different seagrass species sampled in the Mexican Caribbean (*Thalassia testudinum*, Marba et al. 1994a) and the Spanish Mediterranean (*Posidonia oceanica* and *Cymodocea nodosa*, Marba unpubl.), and their age
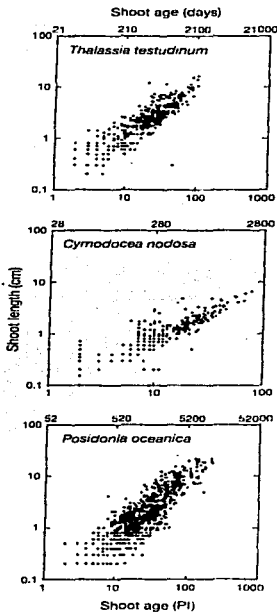
the average number of rhizome internodes produced per PI (rhizome PI; cf. Patriquin 1973, Duarte 1991, Gallegos et al. 1993), which can be translated into rhizome elongation rate by multiplying this slope by the average length of a rhizome internode.

The growth of vertical rhizomes (i.e. short shoots) allows seagrasses to survive sediment accretion (Patriquin 1973, Boudouresque et al. 1984, Eleuterius 1987, Marba et al. 1994a, b) and contribute to rhizome production (Gallegos et al. 1993). Vertical production can also be easily calculated by regressing the length of short shoots (from their insertion on the horizontal rhizome to the apical meristem) against shoot age, with the slope representing the vertical elongation rate (Fig. 9).

Knowledge of rhizome growth rates enables one, in turn, to calculate areal rhizome production as the sum of the production of horizontal and vertical rhizomes. Horizontal rhizome production can be estimated as the product of the elongation rate, the number of growing rhizome apices per unit area, and the specific weight of rhizome material (Patriquin 1973). The areal production of vertical rhizomes can be estimated as the product of their elongation rate, shoot density, and the specific weight of rhizome material (Gallegos et al. 1993). Seagrass roots often appear as a bundle at the insertion of shoots on the rhizomes, and root biomass is linearly scaled to shoot density (Francou & Semroud 1992). Because the number of rhizome internodes in between consecutive shoots is relatively constant and easy to determine (e.g. Patriquin 1973), root production can be calculated as the product of the root weight per unit rhizome biomass and the production of horizontal rhizomes. The production of roots in the vertical shoots can also be estimated by regressing the number or biomass of roots formed against shoot age (Duarte unpubl.).

Reconstruction techniques were first used to measure leaf production of *Zostera marina* by Petersen (1913), and both leaf and rhizome production of *Thalassia testudinum* by Patriquin (1973). Subsequently, they have been used to measure the production of *T. testudinum* in the Mexican Caribbean (Gallegos et al. 1993), to reconstruct the leaf production of the Mediterranean seagrass *Posidonia oceanica* (Pergent & Pergent-Martini 1990), and the rhizome elongation and production rates of *Cymodocea nodosa* (Perez 1989, Duarte & Sand-Jensen 1990a, b, Terrados & Ros 1992). These studies all demonstrate that reconstruction techniques provide reliable estimates of seagrass production, and are powerful tools to expand our knowledge of seagrass growth to remote areas where the repetitive visits required by standard techniques are difficult. They also make large-scale surveys of seagrass growth with limited resources possible.

fence, increased use of reconstruction techniques
should help expand and balance the geographic distri-
bution of our knowledge of seagrass ecology.

Seagrass population dynamics

Seagrasses are modular plants with a continuous
production, and loss, of modules (Tomlinson 1974).
This continuous turnover is most evident for leaves,
and represents the foundation of marking techniques
to estimate seagrass production (Zieman 1974). How-
ever, seagrass shoots are also subject to a continuous
turnover which is reflected by the age structure of the
roots (Duarte & Sand-Jensen 1990b, Gallegos et al
1992, 1993, Perez et al 1994).

Seagrass shoots have an age structure often charac-
terised by few very young shoots with 1 to 2 leaves,
any young (<1 yr old) shoots, and exponentially
declining numbers with increasing shoot age (Fig. 5)
The relative scarcity of very young shoots is likely
accounted for by Patriquin's (1973) observation that
the first leaves on vertical shoots are produced much
faster than subsequent leaves. The exponential decline
in shoot abundance with increasing age results from
shoot mortality and allows estimation of exponential
shoot mortality rates (M, in units time^{-1}) as the nega-
tive slope of the exponential equation.

$$N_t = N_0 e^{-Mt} \qquad (1)$$

where N_0 = number of shoots with age equal to the
mode; and N_t = number of shoots older than modal
shoots by time t. This calculation assumes constant
annual shoot mortality and recruitment rates, and may,
therefore, involve error when this assumption is not
fulfilled (Gallegos et al. 1993). Annual shoot recruit-
ment rates (R_{gross}, in units yr^{-1}) can also be calculated
from the total number of shoots ($\sum_{i=0}^{n} N_i$) and the num-
ber of shoots older than a year ($\sum_{i=1}^{n} N_i$) in the shoot
population (Duarte & Sand-Jensen 1990b, Gallegos et
al 1993) as

$$R_{gross} = \ln \sum_{i=0}^{n} N_i - \ln \sum_{i=1}^{n} N_i \qquad (2)$$

Knowledge of gross recruitment and mortality rate
helps forecast seagrass population dynamics, which
depends on net annual shoot recruitment (R_{net}), since

$$R_{net} = R_{gross} - M \qquad (3)$$

Positive net shoot recruitment rates predict increasing
seagrass density, whereas populations with negative
shoot recruitment rates are in decline (e.g. Duarte
and-Jensen 1990b).

Seagrass rhizomes often decompose slowly (Harri-
son 1989), such that vertical shoots remain attached

to the rhizome for some time after shoot death.
Shoot death generally involves the death of the leaf-
producing meristem in the shoot apex, which appears
to be preceded by a narrowing of the meristem and
production of very thin leaves (Gallegos et al. 1993,
Duarte pers. obs.). Hence dead shoots often can be
differentiated from broken shoots, because they have a
rounded, instead of truncated, apex (e.g. genera Tha-
lassia, Cymodocea, Halodule, Syringodium, Posidonia:
Gallegos et al. 1993, 1994, Duarte pers. obs., Fortes
pers. obs.). The presence of many dead shoots in sea-
grass populations is a consequence of their continuous
turnover and is a convenient tool to reconstruct sea-
grass growth (Gallegos et al. 1993). The median age of
dead shoots represents their median life expectancy
and is, therefore, a useful indicator of shoot turnover
time (Gallegos et al 1993). Indeed, the life expectancy
of shoots indicates the median time for all shoots to die
which should be equivalent, if the seagrass meadow
approaches steady state, to the turnover time of shoots.
Because the shoots appear at regular intervals along
the rhizomes, the shoot turnover time calculated in this
way should be of the same order as the rhizome
turnover time (Gallegos et al 1993)

The frequency distribution of shoot age-at-death is
often fitted much better by an exponential loss function
(Fig 10) than that of living shoots (Fig. 5; Gallegos et al
1993). The reason for this is that the distribution of age-
at-death combines all shoots dying at a particular age
regardless of which year they were produced, hence av-
eraging out interannual variability in recruitment and
mortality (Gallegos et al. 1993). Mortality estimates
derived from the distribution of age-at-death are, there-
fore, more robust than those obtained from the distribu-
tion of living shoots (Gallegos et al. 1993), but represent
average estimates along the life span of the shoots.

Mortality and recruitment estimates are useful to
evaluate the status of seagrass meadows and to fore-
cast their development. Seagrass populations at near
steady state should show a balance between shoot
mortality and recruitment. Deviations towards recruit-
ment rates higher than mortality rates and vice versa
are indicative of expanding and declining populations,
respectively (Duarte & Sand-Jensen 1990b). In addi-
tion, quantification of seagrass shoot life span is a con-
venient estimate of what the average life span of the
rhizome material might be.

Seagrass colonisation and reproduction

Seagrasses often experience mass mortality and sub-
stantial reductions in the extension of their meadows
(Kemp et al. 1983, Cambridge & McComb 1984), which
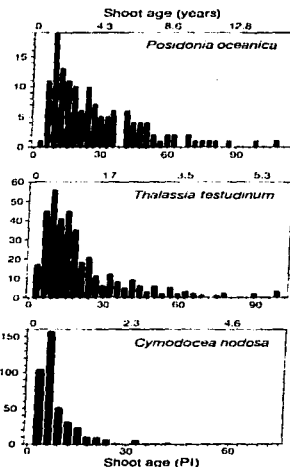has far-reaching consequences in the ecosystem, such

Fig. 10. Frequency distribution of age-at-death of short shoots different seagrasses sampled in the Spanish Mediterranean, (*Posidonia oceanica* and *Cymodocea nodosa*, Duarte unbl.) and the Mexican Caribbean (*Thalassia testudinum*: llegos et al. 1992) showing the exponential decline in shoot number with age that allows calculation of mortality rate

sediment erosion and loss of associated biota (Christensen et al. 1981). Forecasting seagrass colonisation therefore, important to predict ecosystem recovery, ere is, however, a remarkable paucity of quantita- data on the rate of seagrass recovery which pre- ts the development of models to forecast this cess.

econstruction techniques are valuable tools to sure patch formation and patch expansion rates, main processes involved in seagrass recovery

(Duarte & Sand-Jensen 1990a). Seagrass patches often develop by seed dispersal followed by seedling establishment and expansion of the formed patch by rhizome growth (Duarte & Sand-Jensen 1990a). Reconstruction techniques allow calculation of seagrass flowering intensity, which sets an upper limit to the seed production possible. Flowering intensity can often be estimated because identification of flower scars (e.g. genera *Thalassia*, *Cymodocea*, *Enhalus*; Durako & Moffler 1987, Cox & Tomlinson 1988, Gallegos et al. 1993, 1994, Duarte pers. obs., Fortes pers. obs.) or flower peduncles (e.g. Pergent & Pergent-Martini 1990) allows calculation of both the time elapsed since the flower was produced (i.e. number of leaves and leaf scars produced since appearance of the flower scar), and the age at which the shoot flowered (i.e. number of leaf scars from the shoot insertion point to the flower scar, Cox & Tomlinson 1988, Gallegos et al. 1992). Quantitative sampling of seagrass shoots yields, therefore, considerable insight into the reproductive biology of seagrasses, such as calculation of past flower intensity (Pergent et al. 1989, Gallegos et al. 1992) and examination of the age-dependence of shoot flowering (Gallegos et al. 1992).

Flowering intensity is, however, of limited use to assess the potential formation of new patches, which depends on seed production, germination, and the survival and subsequent growth of the seedlings. Yet, seedling production and survivorship can also be estimated using reconstruction techniques (Duarte & Sand-Jensen 1990a). Seagrass seedlings can be easily identified because they often lack rhizome connections to other shoots and because they often retain remains of the seed coat at their base. Seedling age, as estimated from the number of leaves and leaf scars on the short shoot, represents the time elapsed since germination. Estimating net seedling production from quantitative evaluation of seedling abundance is, therefore, straightforward (Duarte & Sand-Jensen 1990a). Moreover, the age distribution of seedlings often presents a sharp exponential decline which allows estimation of seedling mortality rates (see above). Seedling survival, however, is not sufficient to ensure formation of a new seagrass patch, for seedlings may survive without producing horizontal rhizomes and new shoots (Duarte & Sand-Jensen 1990a). The proportion of seedlings producing horizontal rhizomes, as well as the timing of this event, can also be evaluated using reconstruction techniques (Duarte & Sand-Jensen 1990a) which allow, therefore, quantification of different aspects of seedling growth and the establishment of new patches.

Seagrass patches expand through rhizome growth leading to space occupation (Bell & Tomlinson 1980, Duarte & Sand-Jensen 1990a) The maximal rate of patch expansion is set by the maximal rate of horizontal

rhizome elongation, but this capacity is not necessarily realised in natural seagrass patches. The monopodial growth of the rhizomes of many seagrass species (Tomlinson 1974) implies that patches grow centrifugally through long rhizomes (runners), which branch subsequently to occupy the space and increase local density. The rate of patch growth and internal biomass development can also be quantified using reconstruction techniques (Duarte & Sand-Jensen 1990a, b). The location within a seagrass patch where the oldest shoots are encountered represents the site of patch initiation, whenever these are younger than the maximum life expectancy of the species examined (Patriquin 1975, Duarte & Sand-Jensen 1990a). Similarly, the gradient of maximal shoot age along the main axis of seagrass patches provide estimates of the time course of patch growth (Patriquin 1975, Duarte & Sand-Jensen 1990a). The horizontal gradient of maximal age across the patch axes represents, therefore, the patch expansion rate, calculated as the slope of the regression equation relating distance from the patch margin to maximal shoot age (Duarte & Sand-Jensen 1990a).

Seagrass as tracers of sediment transport and chemistry

Seagrasses may inhabit highly dynamic substrates and adapt to sediment accretion, and burial, by the ability to grow vertically (see above) and raise the rhizome meristems to the new sediment level. Seagrasses relocate their meristems closer to the sediment surface after burial by speeding up the vertical growth of their shoots and develop new layers of horizontal rhizomes from meristems in vertical rhizomes (e.g. *Thalassia testudinum*, Tomlinson 1974; *Cymodocea nodosa*, Caye & Meinesz 1985). Patriquin (1973) first noted that the vertical growth of *T. testudinum* shoots differed considerably among populations and suggested that this could be used to estimate sedimentation rates. His suggestion that seagrasses hold potential as tracers of sediment migration was developed further in an examination of the extent and 'migration' of erosional scarps ('blowouts') along *T. testudinum* meadows using age determinations (Patriquin 1975). The close coupling between sediment accretion rates and seagrass vertical growth has been demonstrated since for other turtlegrass meadows off the Yucatan Peninsula (Marbà et al. 1994a), as well as for the Mediterranean species *Posidonia oceanica* (Boudouresque et al. 1984) and *C. nodosa* (Marbà et al. 1994b).

The coupling between seagrass vertical growth and sediment accretion is so close that abrupt changes in the length of the vertical internodes can be used to trace the timing of burial events (Marbà et al. 1994b).

This allowed the estimation of the migration velocity of large-scale subaqueous bedforms over *Cymodocea nodosa* patches in a Mediterranean bay by estimating the time interval between passage of successive dunes over a seagrass patch and following the time course of transit of individual subaqueous dunes over seagrass patches (Marbà et al. 1994b).

In addition to their use as tracers of sediment accretion and erosion, seagrasses are also useful indicators of changes in sediment chemistry. The rhizomes of the long-lived Mediterranean seagrass *Posidonia oceanica* preserved a record of atmospheric caesium fallout, which closely matched that of known atmospheric loading (Fergent et al. 1984, Calmet et al. 1988). This capacity is most useful in long-lived seagrasses, whose tissues remain for decades (e.g. *P. oceanica*, *Enhalus acoroides*, *Thalassodendron ciliatum*). The use of seagrasses as tracers of past chemical environments is probably restricted to compounds not greatly involved in metabolism and rapidly translocated within the plants. Despite the obvious relevance, however, this potential use of seagrasses has not been explored further.

CONCLUSIONS

The ability to determine the age of organisms has proven most useful in elucidating their ecology and population dynamics, as exemplified by the power of tree rings to reconstruct past climates, and the power of growth rings in otoliths and mussel shells to examine organismal growth rate and its interannual variability in relation to known perturbations. Similarly, we demonstrate here that the ability to determine the age of seagrass modules is a strong instrumental tool to reconstruct key components of seagrass dynamics (growth, population dynamics, reproductive effort and recovery rates), as well as to reconstruct processes in their sediment environment.

The use of this set of techniques is restricted to studies focused at annual, or longer, time scales. Accordingly, the approach described here is most powerful when used to examine long-lived seagrass species. Yet, the use of techniques based on age determinations was first demonstrated for *Zostera marina* (Petersen 1913), with rhizome chains lasting only 1 to 2 yr, and we have successfully applied these techniques to study short-lived species (*Halodule wrightii* and *Syringodium filiforme*, Gallegos et al. 1994). We contend, therefore, that techniques based on age determinations should be applicable to most seagrass genera. Hence, reconstruction techniques increase the possibility to improve and increase the balance of our knowledge of the role of seagrasses in the planet's coastal zones.

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NOTE

Growth patterns and demography of pioneer Caribbean seagrasses *Halodule wrightii* and *Syringodium filiforme*

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ABSTRACT: The shoot demography and rhizome growth of *Syringodium filiforme* Kütz. and *Halodule wrightii* Aschers. were studied, based on plant dating techniques, to account for their role as pioneer in the successional sequence of Caribbean seagrasses. Results demonstrated that these species are able to develop dense meadows, supporting biomasses in excess of 500 g DW m⁻². They produced more than 2000 g DW m⁻² yr⁻¹ due to their high leaf (5.0 to 8.5 yr⁻¹) and rhizome (2.0 to 3.3 yr⁻¹) turnover. Rhizome growth and branching rates were very high, allowing these seagrasses to rapidly occupy the space they colonize. The rapid rhizome turnover involved, however, a high shoot mortality rate and low life expectancy (average shoot life expectancy 100 to 180 d). This implies that, while these pioneer species are able to rapidly occupy the space they colonize, their established shoots cannot occupy that space for as long as the more long-lived species *Thalassia testudinum*. We suggest, therefore, that the role of seagrass species as pioneer or climax species is independent of their capacity to support dense, productive populations, and is closely related to shoot longevity and rhizome turnover.

KEY WORDS: Rhizome growth · Shoot age · Biomass · Production

The seagrasses *Syringodium filiforme* Kütz. and *Halodule wrightii* Aschers. occupy an important role as pioneer species in the Caribbean Sea (den Hartog 1971, Patriquin 1975). They colonize denuded sediments following perturbations, preceding the climax community of *Thalassia testudinum* Banks ex König in the successional sequence of Caribbean seagrasses (den Hartog 1971, Patriquin 1975, Williams 1987, 1990). *S. filiforme* and *H. wrightii* also develop mono-

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specific meadows in the area (Gilbert & Clark 1981, Iverson & Bittaker 1986, Van Tussenbroek 1994), so that, in addition to their role as pioneer species, they may also be important primary producers (Zieman et al. 1989, Short et al. 1993). Most studies on these species have focused on leaf biomass and production (Virnstein 1982, Fry 1983, Barber & Behrens 1985, Iverson & Bittaker 1986, Eleuterius 1987, Williams 1987, Fry & Virnstein 1988, Zieman et al. 1989, Van Tussenbroek 1994), and reports of their rhizome growth and demography are as yet few (Eleuterius 1987, Zieman et al. 1989, Marbà et al. 1994). Knowledge of their rhizome growth rates and demographic dynamics would, however, help to interpret the dynamics and maintenance of the meadows these species develop (Duarte & Sand-Jensen 1990a, b).

On the basis of data obtained using plant dating techniques (Patriquin 1973, Gallegos et al. 1993, Duarte et al. 1994, Marbà et al. 1994), we describe the biomass, and rhizome and shoot dynamics of monospecific *Syringodium filiforme* and *Halodule wrightii* meadows in the Mexican Caribbean.

Methods. We studied shallow (1.0 to 1.5 m) monospecific meadows of *Syringodium filiforme* and *Halodule wrightii* on the reef lagoon near the town of Puerto Morelos (21° N, 87° W, Yucatán Peninsula, Mexico, Marbà et al. 1994), using the approach described by Gallegos et al. (1993). In August 1991, the time of maximum seagrass biomass in the area (Van Tussenbroek 1994), we randomly collected 6 and 3 cores (20.5 cm internal diameter) from the *S. filiforme* and *H. wrightii* meadows, respectively. The cores were pushed 40 cm into the sediment to collect the shoots down to their insertion in the rhizomes, which was needed to esti-

male shoot age (cf. Gallegos et al. 1993). Sediment (coarse carbonate sand) was then carefully washed off the samples, all the living shoots and the standing leaves they supported were counted, and the presence of flowers or fruits recorded. We also noted the number of branches in the horizontal rhizomes as well as the number and length of rhizome internodes between consecutive shoots and those in the entire sample, to estimate rhizome growth (cf. Gallegos et al 1993).

The age of living (i.e. bearing green leaves) and dead (i.e. devoid of green leaves) shoots was estimated as the sum of the number of leaf scars and standing leaves (Patriquin 1973, Cox & Tomlinson 1988, Gallegos et al. 1993). Dead shoots were dated only if they ended in a rounded tip, indicating that the shoot was not broken (Gallegos et al. 1993). The age units obtained were plastochrone intervals (PIs), which represent the average time interval between the initiation of 2 successive leaves on a shoot (Erickson & Michelini 1957, Brouns 1985). Using a dissecting microscope, we examined the time course of vertical internodal length of the oldest shoots sampled, to identify annual cycles in the length of vertical internode (cf. Duarte et al 1994, Marbà et al. 1994). The inverse of the number of internodes in a cycle (number of leaves yr⁻¹) corresponds to the annual average PI (cf. Duarte et al. 1994, Marbà et al. 1994) which was used to convert PIs into absolute time units.

The data set obtained in August 1991 was complemented with information on flowering frequency, maximal shoot age, and additional sequences of internodal length for old shoots. These were obtained during 2 more visits in the spring of 1992 and 1993 (sample sizes about 2000 and 4000 shoots for *Syringodium filiforme* and *Halodule wrightii*, respectively).

The PI of horizontal rhizomes was calculated by regressing the number of rhizome internodes between shoots along the rhizome against their age difference (Patriquin 1973, Gallegos et al 1993). The rate of vertical growth of *Syringodium filiforme* and *Halodule wrightii* shoots was also calculated by regressing shoot length against age (Gallegos et al 1993). Shoot age structure was described using data on living and dead shoots (Gallegos et al. 1993, Duarte et al. 1994). The average age of living shoots represents the overall age of the shoot population, but it does not overestimate their life expectancy, which is best represented by the age at death (Gallegos et al. 1993, Duarte et al. 1994). Shoot mortality (K, in natural logarithm units time⁻¹; cf. Duarte & Sand-Jensen 1990b) was calculated from the age distribution of dead shoots (Gallegos et al. 1993, Duarte et al.

1994) by fitting the equation

$$N_t = N_0 e^{-Kt}$$

which describes the exponential decline in shoot number (N) in increasingly older age classes with time (t) from the onset on mortality (t = 0). Shoot recruitment rates were then calculated as the natural logarithm of the inverse of the fraction of the shoot population older than 1 yr (Duarte & Sand-Jensen 1990b).

Results. *Halodule wrightii* and *Syringodium filiforme* developed lush monospecific stands in the reef lagoon, reaching a high shoot density and high biomass of shoots and rhizomes (Table 1). Rhizome internodes of *S. filiforme* were thicker and longer than those of *H. wrightii* (30.6 + 0.25 and 20.2 ± 1.0 mm internode⁻¹, respectively), and the 2 species formed a dense network of 228.5 m and 216.8 m of rhizome m⁻², respectively. Shoot density closely resembled rhizome internode density (Table 1), because both species produce 1 short shoot at each rhizome internode. The number of internodes between connected shoots and their age difference were closely correlated (p < 0.0001). The slope of the regression equations describing these relationships indicated that *H. wrightii* and *S. filiforme* produce 1.81 ± 0.17 and 2.81 ± 0.27 internodes PI⁻¹, respectively Shoot vertical growth was calculated from regression analysis between shoot length and shoot age to be 0.56 ± 0.13 and 0.12 ± 0.01 cm PI⁻¹ for *S. filiforme* and *H. wrightii*, respectively (Fig. 1). The distinct seasonal pattern in the sequence of vertical internodal length (Fig. 2) allowed calculation of the average number of vertical internodes (= number of leaves) produced per shoot per year, and the average PI for the 2 species (Table 1), which were used to calculate annual rates of rhizome elongation from rates per PI (Table 1). Rhizomes branched in 3.2% and 9.3% of the rhizome

Table 1. *Syringodium filiforme* and *Halodule wrightii*. Average (± SE) shoot and rhizome biomass, density, production, and mortality rates for the populations studied

Variable	S. filiforme	H. wrightii
Shoot biomass (g DW m⁻²)	446.9 + 48.4	519 ± 86
Shoot density (shoots m⁻²)	7139 ± 1366	14872 ± 2444
Rhizome biomass (g DW m⁻²)	233	97
Rhizome density (internodes m⁻²)	7468	10742
Leaf plastochrone interval (d)	60.8	16.5
Leaves shoot⁻¹ yr⁻¹	6	22.1
Rhizome elongation (cm yr⁻¹ apex⁻¹)	51.6	80.9
Vertical growth (cm yr⁻¹ shoot⁻¹)	3.36	2.65
Shoot recruitment (ln units yr⁻¹)	0.77	4.18
Shoot mortality rate (ln units yr⁻¹)	2.04 + 0.39	3.54 ± 0.37
Leaf production (g DW m⁻² yr⁻¹)	2234	4619
Rhizome production (g DW m⁻² yr⁻¹)	468	320

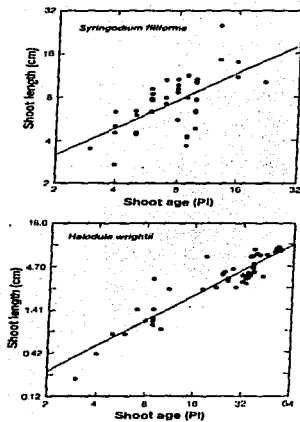Fig. 1. *Syringodium filiforme* and *Halodule wrightii*. Relationship between the length of vertical rhizomes and the age of shoots

Fig. 2. *Syringodium filiforme* and *Halodule wrightii*. Sequence of internodal length recorded for the oldest shoots sampled. Arrows indicate annual cycles

internodes examined for *S. filiforme* and *H. wrightii*, respectively.

The average age of *Syringodium filiforme* shoots was ca 1 yr (6.7 ± 0.1 Pls), and most of the shoots had been produced within the current year (i.e. age <7 Pls; Fig. 3), indicative of a high shoot recruitment rate (Table 1). The age distribution of dead shoots (Fig. 3) showed a clear exponential decline in survival with increasing age that allowed calculation of mortality rates (Table 1). The average life expectancy of *S. filiforme* shoots was found to be about half a year (3 ± 0.16 Pls) and the oldest *S. filiforme* shoot found was about 7 yr (46 Pls, n > 2000). Almost all of the living *Halodule wrightii* shoots had been produced within a year (Fig. 4), indicating very high shoot recruitment rates (Table 1). High rates are needed to compensate
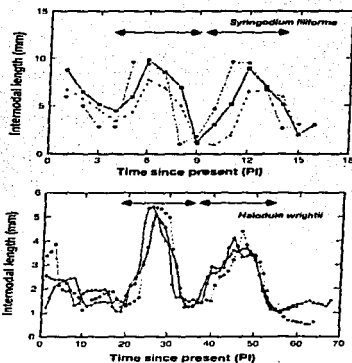
for their high mortality rate (Table 1), as reflected by the rapid exponential decline in shoot abundance with increasing shoot age (Fig. 4). The life expectancy of *H. wrightii* shoots is, therefore, only about 3 mo or 6.9 ± 0.4 Pls, and the longest-lived shoot found was only 3 yr (70 Pls, n > 4000).

The average shoot life expectancies estimated (182 and 110 d for *Syringodium filiforme* and *Halodule wrightii*, respectively) will, in a stable population, correspond to their shoot turnover time (Gallegos et al. 1993), which are, therefore, about 2.0 and 3.3 yr^{-1}. These estimates should also be close to the average rhizome turnover rates (Gallegos et al. 1993), because shoot turnover is maintained by a parallel rhizome turnover (i.e. 1 internode is formed for each shoot produced). An estimate of the average number of leaves that a shoot produces per year, together with the average number of standing leaves per shoot (2.6 ± 0.1 and 1.2 ± 0.03 leaves shoot^{-1}), allows the leaf turnover to be calculated as 8.5 and 5.0 yr^{-1} for *H. wrightii* and *S. filiforme*, respectively. Hence, leaf turnover is about twice
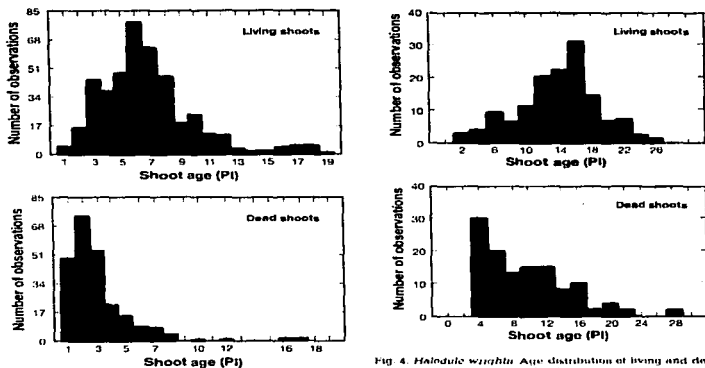
Fig. 3. *Syringodium filiforme*. Age distribution of living and dead shoots

Fig. 4. *Halodule wrightii*. Age distribution of living and dead shoots

s fast as rhizome turnover. The calculated turnover ates combined with the biomass of leaves and rhizomes (Table 1), which show little seasonal variation in his area (Van Tussenbroek 1994), reveal the production of the 2 species to be nearly 3 and 5 kg DW m^{-2} r^{-1}, respectively (Table 1).

Syringodium filiforme and *Halodule wrightii* flowered in spring, and 6.4 % and 10.5 %, respectively, of heir shoots had flowered in spring 1993, representing bout 300 and 1500 flowering shoots m^{-2}, respectively. Flowering shoots had an average age of 8.4 ± 0.8 PI for *S. filiforme* and 29.3 ± 2.7 PI for *H. wrightii*, which indicates flowering to be more frequent for shoots older han 1 yr. In August 1991, 366 fruiting *H. wrightii* hoots m^{-2} were found, with each fruit-bearing shoot aving 2 fruits, which indicates that only about 20% of he flowering shoots set fruit.

Discussion. The results obtained showed that the 2 pecies are able to develop lush, highly productive neadows in the Mexican Caribbean (Table 1). The hoot density and biomass were greater than values

reported to date for the Gulf of Mexico (e.g. Eleuterius 1987) and the Atlantic Ocean (Short et al. 1993), although *S. filiforme* has been observed to produce even larger biomasses, close to 1 kg DW m^{-2}, in the Mexican Caribbean (Van Tussenbroek 1994). The biomass and production of *S. filiforme* and *H. wrightii* (Table 1) were each comparable to that of *T. testudinum*, the climax species, in this area (Gallegos et al. 1993).

The 2 populations of *Syringodium filiforme* and *Halodule wrightii* studied had higher horizontal elongation rates (Table 1) than those reported in the northern Gulf of Mexico (Eleuterius 1987), although *S. filiforme* rhizomes grew at rates similar to that reported for the Indian River Lagoon (Florida, USA; Short et al. 1993). Rhizome growth rates for the species investigated were 2- to 4-fold greater than those of *Thalassia testudinum* in the Caribbean (22.3 cm yr^{-1}; Gallegos et al. 1993). In addition to their higher growth rate, *S. filiforme* and *H. wrightii* also branched at every 94 and 21.8 cm, respectively, whereas *T. testudinum* produces 1 branch for every 6300 cm of horizontal rhizome (Gallegos et al. unpubl.). Hence, *S. filiforme* and *H. wrightii* are able to colonise and occupy space much faster than

T. testudinum. Moreover, the density of flowering *H. wrightii* and *S. filiforme* shoots is about 10- to 50-fold greater than that of *T. testudinum* (Gallegos et al. 1992, 1993), further contributing to the ability of these species to colonise unvegetated sediments faster than the climax species.

The high growth rate and associated high mortality rate of *Syringodium filiforme* and *Halodule wrightii* (Table 1) imply that these pioneer species must have high nutrient requirements (Fourqurean et al. 1992, Short et al. 1993, Duarte 1994). The rapid loss of *S. filiforme* and *H. wrightii* material, which represents the bulk of the abundant seagrass material washed onto the shoreline, associated with the short life-span of their leaves and shoots, must also reduce their capacity for nutrient storage and internal recycling. In contrast, *Thalassia testudinum* grows slower and lives much longer (Gallegos et al 1993), and should, accordingly, have lower nutrient requirements (Fourqurean et al. 1992, Duarte 1994), and be better able to store and recycle nutrients (Patriquin 1972).

These observations help explain why *Thalassia testudinum* is the climax species in the Caribbean, and why the dense meadows developed by *Syringodium filiforme* and *Halodule wrightii* are eventually replaced by meadows of the longer-lived climax species in oligotrophic Caribbean ecosystems. Our results also demonstrate important differences in the reproductive output and rhizome growth of the 2 pioneer species. The areal density of *H. wrightii* flowering shoots was 5-fold greater than that of *S. filiforme*, which also had a slower rhizome growth and turnover. Hence, *S. filiforme* presents an intermediate reproductive effort, rhizome turnover, and shoot longevity between *H. wrightii* and *T. testudinum*, and indeed occupies an intermediate position in the Caribbean seagrass successional sequence (den Hartog 1971, Williams 1990).

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