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Ecofisiología de Asociaciones
Micorrícicas Arbusculares
en Especies Pioneras de un
Ecosistema de Dunas Costeras
del Golfo de México

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En las dunas costeras, las plantas pioneras están sujetas a considerable "stress" debido a los bajos niveles de nutrimentos, la amplia fluctuación en la humedad y temperatura del suelo, el enterramiento o exposición a erosión por viento y el daño por aspersión salina y ráfagas de arena. Por lo tanto se considera que cualquier factor que mejore la toma de nutrimentos o ayude a la estabilización del sustrato puede contribuir al establecimiento de la vegetación en este tipo de ecosistemas.

Se ha demostrado que el micelio externo de los hongos micorrícicos arbusculares (MA) juega un papel muy importante en el proceso de estabilización al unir los granos de arena, formando agregados más resistentes al viento. Sin embargo, aunque se ha reconocido el papel de las micorrizas en el incremento de la captura de fósforo y su efecto en la mayor tasa de crecimiento de las plantas, los estudios realizados al respecto, en plantas colonizadoras de dunas son contados. Más aún, la mayor parte de las investigaciones realizadas sobre micorrizas en estos ecosistemas provienen de zonas templadas.

Dentro del Centro de Investigaciones Costeras de la Mancha (CICOLMA) existe un sistema de dunas con una gran heterogeneidad ambiental en donde se distribuye una amplia diversidad de especies. Debido a que en este sistema no se han realizado estudios sobre asociaciones micorrícicas arbusculares, la primera parte de este trabajo consistió en determinar la condición micorrícica de las especies que se distribuyen en sus diferentes estadios sucesionales. Los resultados indicaron que el 97% de las especies que se recolectaron estuvieron asociadas con hongos micorrícicos arbusculares, incluyendo especies pertenecientes a familias esencialmente no-micotróficas como Aizoaceae, Convolvulaceae, Commelinaceae y Cyperaceae.

Los altos porcentajes de colonización por hongos MA encontrados en este sistema y en otras dunas costeras del mundo, han cuestionado las teorías existentes sobre el papel de las micorrizas en la sucesión primaria. Con base en estos resultados, se estableció como objetivo general de la tesis, analizar el efecto de las asociaciones micorrícicas arbusculares en el crecimiento de plantas pioneras de este sistema tropical de dunas costeras.

A continuación se reportan los experimentos que se establecieron tanto en el sistema natural como en el invernadero y los resultados obtenidos:

1) Potencial de inóculo micorrícico de la arena de la playa y de diferentes estadios sucesionales del sistema de dunas (móvil, pastizal, matorral)

Se recolectó arena en el área de la rizósfera de las plantas distribuidas en la playa y en diferentes estadios sucesionales de las dunas (móvil, pastizal y matorral). Con la arena de cada una de estas zonas se prepararon macetas en donde se sembró maíz. Se hicieron 2 cosechas (a los 8 días y 1 mes después del trasplante) de 3 réplicas por cada sitio. Se registró el porcentaje de colonización en las raíces de cada una. Ocho días después del trasplante, el porcentaje de colonización por hongos MA fue un promedio de 10% y no hubo diferencias significativas entre las zonas. En la segunda cosecha, un mes después del trasplante, el menor potencial de inóculo se registró en la zona móvil y el mayor en la del matorral.

2) Velocidad de colonización por hongos micorrícicos arbusculares en la zona de pioneras y móvil

Se sembraron plántulas de Chamaecrista chamaecristoides de 5 días de edad en cuadros establecidos al azar en la zona de pioneras, en la zona móvil y en un pastizal del sistema de dunas. Se recolectaron 5 plántulas por cuadro cada semana para comparar el tiempo que se requiere para que se establezca la asociación micorrícica en cada zona.

En la zona de pioneras se observaron arbusculos desde la segunda semana y vesículas y arbusculos en la tercera semana. En la zona móvil no se detectó colonización por hongos MA durante las tres semanas del experimento.

3) Efecto de micorrizas arbusculares en el crecimiento de especies colonizadoras del sistema de dunas costeras de la Mancha, Veracruz

Se realizó un experimento en el invernadero de la estación del CICOLMA con especies que se distribuyen en la playa, dunas embrionarias, dunas móviles y/ o semi-móviles. Todas las plantas se sometieron a dos tratamientos: presencia (+M) y ausencia de micorrizas (-M). Se realizaron tres cosechas: una cosecha inicial, otra a los 21 días después del trasplante y la cosecha final a los 63 días después del trasplante. Utilizando las mediciones del área foliar y el peso seco de la raíz, el tallo y las hojas se compararon los siguientes parámetros del crecimiento entre las plantas +M y -M: la biomasa seca total, la tasa de crecimiento (R), la tasa de asimilación neta, los patrones de asignación de biomasa (Proporción raíz/parte aérea (R/S), proporción de raíz (RWR), tallo (SWR) y hojas (LWR) en la biomasa seca total) y el porcentaje de dependencia micorrícica (de acuerdo a Plenchette 1983) en las condiciones probadas.

En las plantas que se cosecharon 21 días después del trasplante, no se observaron diferencias significativas entre los dos tratamientos en la biomasa seca total. Sin embargo, en la cosecha final se registraron “dependencias micorrícicas” diferentes entre las especies (Ipomoea pes-caprae -10%, Sporobolus virginicus (-6%), Canavalia rosea (27%), Palafoxia lindenii (64%), Panicum purpurascens (64%), Trachypogon gouinii (84%).

I. pes-caprae, C. rosea y S. virginicus, las especies con menores respuestas en producción de biomasa hacia la inoculación con hongos micorrícicos, son especies rastreras cuya distribución está restringida a la playa y dunas embrionarias. Sus respuestas apoyan las teorías que plantean que las etapas serales tempranas son colonizadas por plantas no-micorrícicas o con dependencias menores de las asociaciones micorrícicas. Sin embargo, los altos incrementos en producción de biomasa de C. chamaecristoides, T. gouinii y P. lindenii, podrían indicar que las micorrizas también son esenciales para el crecimiento de especies que se desarrollan en los primeros estadios de la sucesión.

Abstract

Root samples of 37 species distributed along a successional gradient in a tropical sand dune system on the Gulf of Mexico were collected to determine their mycorrhizal status. Since 97% of the species were recorded as mycorrhizal, our results support the high arbuscular mycorrhizal status found in other dunes of the world.

To determine the mycorrhizal inoculum potential (MIP) of sand, two bioassays were set. The first one was conducted by transplanting maize seedlings to pots previously filled with sand from the foredunes, mobile dunes, grassland and a Dyphisa robinoides shrub area. The lowest MIP was found in the mobile dunes and the highest in the shrub area. The second bioassay was conducted in field conditions, by transplanting Chamaecrista chamaecristoides seedlings in the foredunes and mobile dunes. In the mobile area, no infection was registered during the 21 days of the experiment. In the foredunes, hyphae and external mycelium were present in 40% of the seedlings since eight days after transplanting. Arbuscules and hyphae were observed in 60 and 20% of the seedlings respectively, 15 days after transplanting and in 46 and 20%, 21 days after transplanting.

The effects of AM fungi on the growth of species distributed in different successional stages of a tropical sand dune system were investigated in 21 and 63 day old plants of seven species. The leaf area and the dry biomass of root, stem and leaves of mycorrhizal (+M) and non-mycorrhizal (-M) plants were used to calculate and compare their total dry biomass, relative growth rate, net assimilation rate, biomass allocation patterns (root/shoot, root, stem and leaf weight ratios) and percentages of mycorrhizal dependency (MD). Twenty one days after transplanting, there were no significant differences between +M and -M plants in the root, stem and leaf dry biomass. However, forty days later, a range of mycorrhizal responsiveness was evident in the different early successional species. Ipomoea pes-caprae, Sporobolus virginicus and Canavalia rosea, all stoloniferous species, the distribution of which is restricted to the beach, embryo dunes and foredunes, were the less responsive plants to the mycorrhizal treatment, following the trend predicted for some early seral species (MD = -10, -6, 27% respectively). However, the high increases in dry weight, leaf area and relative growth rate of Palafoxia lindenii, Chamaecrista chamaecristoides and Trachypogon gouinii, plants that could be found in the beach, embryo dunes and foredunes as well as in mobile dunes, suggest that mycorrhizal infection could also be crucial for the early growth of pioneer species (MD = 64, 77, 84% respectively)

"Perhaps no topographic form is more unstable than a dune"
(Cowles 1899)

1. Introducción

Como en muchos ambientes de sucesión primaria, en las dunas costeras las plantas pioneras están sujetas a niveles muy severos de "stress" debido a los bajos niveles de nutrientes (nitrógeno, fósforo y potasio) y materia orgánica, así como a las amplias fluctuaciones en la humedad y temperatura del suelo (Miles & Walton 1993). Adicionalmente, en estos ecosistemas, las plantas están expuestas a episodios de enterramiento o exposición por la erosión por viento y al daño por aspersión salina y ráfagas de arena (Chapman 1976; Moreno-Casasola 1982; Barbour et al. 1985; Maun 1994). Con base en esto se considera que cualquier factor que mejore la captura de nutrientes y de agua o que influya en la estabilización del sustrato, podría contribuir en la sobrevivencia y el establecimiento de la vegetación en este tipo de ecosistemas (Koske et al. 1975; Read 1989).

Las asociaciones micorrícicas constituyen un medio por el que la mayor parte de las plantas suple parte de sus requerimientos de agua y nutrientes, particularmente cuando éstos son recursos limitantes para su crecimiento (Daft & Nicolson 1969; Harley & Smith 1983; Brundrette 1991). Los hongos son excelentes exploradores y colonizadores oportunistas de una amplia gama de sustratos. Debido a su talo filamentoso y al diámetro reducido de sus hifas, se ramifican y se extienden apicalmente formando superficies extensivas (Kendrick 1991). Los hongos micorrícicos por lo general capturan la mayor parte de los recursos inmóviles, como el fósforo, e incrementan la captura de los móviles (Brundrette 1991). Se ha planteado, que al incrementar la disponibilidad de los recursos, las micorrizas pueden influir tanto en el crecimiento de las plantas como en su adecuación (Allen 1991).

Un porcentaje muy alto de las plantas que se distribuyen en dunas costeras están asociadas con hongos micorrícicos arbusculares (Koske & Halvorson 1981; Giovannetti & Nicolson 1983; Giovannetti 1985; Koske & Halvorson 1989; Logan et al. 1989; Koske & Gemma 1990). El micelio externo de estos hongos, juega un papel muy importante en el proceso de estabilización de las dunas, ya que las hifas unen los granos de arena mecánicamente, formando agregados más resistentes al viento (Koske et al. 1975; Sutton & Sheppard 1976; Clough & Sutton 1978; Forster 1979; Forster & Nicolson 1981 a, b). Se ha demostrado que tanto el micelio, como la colonización micorrícica y la abundancia de esporas varían respecto a la posición y la estación en las dunas (Nicolson 1960; Nicolson & Johnston 1979; Jehne & Thompson 1981; Giovannetti & Nicolson 1983; Puppi et al. 1986; Gemma & Koske 1988; Gemma et al. 1989).

Los altos porcentajes de colonización por hongos micorrícicos arbusculares encontrados desde la línea de mareas en algunos sistemas de dunas costeras (Koske & Gemma 1990; Gemma & Koske 1992), han cuestionado las teorías clásicas sobre el papel de las micorrizas en la sucesión (Janos 1980). En éstas se ha planteado que en las primeras etapas serales las plantas por lo general son no-micotróficas o facultativamente micotróficas, mientras que en las etapas serales tardías son reemplazadas por plantas micotróficas obligadas (Janos 1980).

Considerando la hipótesis de Webley et al. (1952), en donde se considera que el desarrollo de los microorganismos es uno de los factores cruciales para la sucesión de las dunas, el objetivo de este trabajo es aportar evidencias al respecto, analizando el efecto de las micorrizas en el crecimiento de plantas colonizadoras de un sistema de dunas costeras.

Dentro del Centro de Investigaciones Costeras de La Mancha (CICOLMA), en el Golfo de México, existe un ecosistema tropical de dunas con una gran heterogeneidad ambiental en donde se distribuye una amplia diversidad de especies (Moreno-Casasola et al. 1982; Moreno-Casasola & Espejel 1986). En este sistema se han realizado muy pocas investigaciones sobre asociaciones micorrícicas (Salas 1994; Pérez 1995). Por lo tanto en

este trabajo se incluye un estudio descriptivo sobre la presencia de hongos micorrícicos arbusculares en plantas que se distribuyen en el mismo y un estudio experimental en donde se analiza el efecto de las micorrizas en la primera etapa del crecimiento de siete especies colonizadoras de este ecosistema de dunas.

Para cumplir con estos objetivos, se establecieron experimentos en el sistema natural y en el invernadero, con especies que se distribuyen en la playa y en diferentes estadios sucesionales, algunas de distribución restringida en las primeras etapas serales, otras que también pueden encontrarse en las zonas estabilizadas (Moreno-Casasola et al. 1982; Moreno-Casasola & Espejel 1986; Moreno-Casasola 1988).

Las preguntas que se plantearon para el desarrollo de esta investigación son las siguientes:

- * ¿Las plantas que se distribuyen en el sistema de dunas de la Mancha, están colonizadas por hongos micorrícicos arbusculares?
- * ¿La arena de la playa y de diferentes zonas sucesionales (móvil, patizal, matorral) tiene diferentes potenciales de inóculo?
- * ¿Existen diferencias entre los porcentajes de colonización por hongos micorrícicos arbusculares que se registran en la playa, la zona móvil y el pastizal?
- * ¿Cuál es la velocidad de colonización por hongos micorrícicos arbusculares en la playa y la zona móvil de las dunas?
- * ¿Cuál es el efecto de las asociaciones micorrícicas en el crecimiento de las plantas colonizadoras de las dunas?
- * ¿Qué diferencia hay en la respuesta hacia la micorriza en plantas que se distribuyen en diferentes zonas de las dunas?
- * ¿Qué parámetros del crecimiento alteran las micorrizas?
- * ¿Cómo responden las plantas a las micorrizas en cuanto a su asignación de biomasa?

Para contestar las preguntas anteriores se plantearon los siguientes objetivos particulares:

- 1) Determinar la condición micorrícica de 37 especies que se distribuyen en la playa y en diferentes etapas sucesionales del sistema de dunas de CICOLMA (dunas embrionarias, zona móvil y semi-móvil, zonas estabilizadas).
- 2) Determinar el porcentaje de colonización por hongos micorrícicos arbusculares en 3 especies endémicas (Chamaecrista chamaecristoides, Palafoxia lindenii y Trachypogon gouinii) que se distribuyen en diferentes zonas de las dunas (playa, duna móvil, pastizal) durante la época de lluvias y secas.
- 3) Determinar el potencial de inóculo micorrícico de la arena de diferentes zonas sucesionales (móvil, pastizal, matorral) y de la playa.
- 4) Conocer la velocidad de colonización por hongos micorrícicos arbusculares en las zonas de la playa y la duna móvil.
- 5) Analizar el efecto de las micorrizas arbusculares sobre el crecimiento de especies colonizadoras del sistema de dunas.

Hipótesis:

*Al igual que la mayor parte de los ecosistemas de dunas que se han estudiado, un alto porcentaje de las especies que se distribuyen en las dunas costeras de la Mancha están asociadas con hongos micorrícicos arbusculares.

*El potencial de inóculo de la arena de las diferentes zonas sucesionales se incrementa con la estabilización del sustrato. Las zonas estabilizadas (pastizal y matorral) deberían tener potenciales de inóculo mayor que las áreas de plantas pioneras (playa y duna móvil).

*Existe un patrón sucesional en los porcentajes de colonización micorrícica. Estos deberían ser mayores en las zonas estabilizadas en comparación con las pioneras.

*Existe un patrón estacional en los porcentajes de colonización micorrícica. Estos deberían ser mayores en la época de lluvias en comparación con la de secas.

*En condiciones de bajos niveles de nutrientes, las plantas asociadas con hongos micorrícicos arbusculares presentan mayores tasas de crecimiento que las que no son inoculadas.

2. Antecedentes

2.1) Las dunas costeras

Las dunas costeras son acumulaciones de arena cuya forma, tamaño y orientación está en función de diversos factores. Entre éstos se encuentran el tamaño de las partículas, las condiciones climáticas (tanto pasadas como presentes), la dirección y velocidad de los vientos dominantes, así como las características ecológicas que determinan la distribución de la vegetación asociada (Moreno-Casasola 1982; Moreno-Casasola et al. 1982; Nordstrom et al. 1990).

La formación de las dunas comienza en la línea de mareas, con la arena que proviene de las superficies expuestas por la marea baja (Chapman 1976). El viento transporta constantemente los granos de arena, los cuales se depositan cuando éste disminuye su velocidad al encontrar un obstáculo, como el que forma la vegetación. La arena se acumula en montículos que forman inicialmente las dunas embrionarias. Posteriormente, se unen y forman cordones de dunas, que pueden ser de formas y alturas muy variables. Conforme la cobertura vegetal se incrementa, los sistemas de dunas se van estabilizando gradualmente (Chapman 1976; Moreno-Casasola 1982; Martínez et al. 1993).

Una vez que las dunas han sido colonizadas, puede haber erosión, y la cobertura vegetal se rompe o se destruye completamente. Cuando esto ocurre, el viento acarrea la arena expuesta y provoca subsecuentes movimientos de arena principalmente en el centro de la duna. De esta manera, la parte central de la duna sigue creciendo y avanzando y se forman las dunas móviles (Ranwell 1972; Chapman 1976).

Las dunas parabólicas o de media luna surgen como resultado de la erosión por viento de las formas fijadas o cuando el suministro de arena es excesivo y la cobertura vegetal es inadecuada (Chapman 1976; Doing 1985). En este tipo de dunas se pueden distinguir diferentes zonas topográficas que presentan características particulares de

acuerdo con su pendiente, exposición al viento, salinidad y movimiento de arena. Estas son los brazos, las cimas o crestas, las pendientes de barlovento y sotavento y las hondonadas (secas, húmedas o inundables) (Chapman 1976; Doing 1985; Moreno-Casasola 1982).

La variabilidad topográfica y el gradiente de recursos que surge por las diferentes distancias de cada zona respecto al mar, crea un mosaico ambiental con distintos microhabitats. Esto provoca que la vegetación se distribuya en parches de diferente estructura y composición (Moreno-Casasola et al. 1982; Ehrenfeld 1990; Martínez et al. 1993). Por otra parte, debido a los factores de perturbación recurrente, en un mismo sistema de dunas coinciden temporalmente, fases estabilizadas con fases móviles que representan diferentes etapas sucesionales (Martínez et al. 1993).

La composición de las especies vegetales de las diferentes zonas de las dunas, varía ampliamente entre las regiones geográficas, desde las templadas hasta las tropicales. Sin embargo, pueden observarse ciertos patrones comunes en los arreglos de los tipos de vegetación. Dentro del gradiente de estabilización se puede observar una zona de pioneras que coloniza la playa; una zona de pastos, arbustos o especies rastreras que forma las dunas embrionarias; zonas de dunas internas en las cuales los arbustos son reemplazados por vegetación herbácea y el desarrollo de diferentes tipos de vegetación en hondonadas entre las crestas de las dunas (Ehrenfeld 1990). De esta manera, dentro del paisaje de los sistemas de dunas se puede observar la playa, las dunas embrionarias y dunas transversales o cordones de dunas, en los que se pueden distinguir zonas móviles y semi-móviles, así como zonas más estabilizadas de pastizales y matorrales y en algunos casos hasta selvas, como sucede en el Golfo de México (Moreno-Casasola et al. 1982; Moreno-Casasola & Espejel 1986; Moreno-Casasola 1988; Martínez et al. 1993).

2.2) El ambiente en las dunas

Como medio de sucesión primaria, la arena de las dunas es un sustrato sin una historia previa de colonización. Por lo tanto, presenta niveles muy bajos de materia orgánica y de nutrimentos, particularmente nitrógeno y fósforo (Willis & Yemm 1961; Barbour et al. 1985; Davy & Figueroa 1993; Maun 1994). En los ecosistemas de dunas de Gran Bretaña se han registrado concentraciones de nitrógeno de 0.006 a 0.02% (Willis et al. 1969), en el Pacífico de 0.003 a 0.001% (Holton 1980), en Lake Huron sólo trazas (Maun 1985) y en el Golfo de México promedios de 0.007% en la zona de pioneras (Moreno-Casasola et al. 1982) y de 68 a 99 ppm de nitrógeno total (Martínez 1992; Valverde 1992; Salas 1994). Por otra parte, los niveles de fósforo registrados en suelos de dunas pueden ser tan bajos como 0.0068 (Atkinson 1973), 0.0001 (Maun 1985), 0.11% (Willis *et al.* 1959) y 35.1 ppm (Salas 1994).

El suministro de nutrimentos inorgánicos, especialmente de nitrógeno, depende de la mineralización de la materia depositada por el mar y de la aspersion salina. Esta última también es una fuente importante de sodio, magnesio, calcio, potasio, nitrógeno y fósforo (Barbour et al. 1985; Kellman & Roulet 1990). Sin embargo, la porosidad tan alta de la arena hace que la retención de agua sea muy baja y que los nutrimentos minerales sean lixiviados con gran facilidad (Chapin 1993; Maun 1994; Kellman & Roulet 1990). Tanto la cantidad de nutrimentos y materia orgánica en el suelo como la capacidad de retención de agua se incrementan durante el proceso sucesional (Valverde 1992; Martínez et al. 1993). Adicionalmente, debido a la baja cobertura vegetal, no hay protección de la alta radiación solar en la superficie del suelo. Esto causa fluctuaciones extremas de temperatura y hace que el sustrato se seque muy rápido.

Además de estar sujetas a estas condiciones ambientales, las plantas pioneras de las dunas costeras deben de tolerar episodios de enterramiento con arena como resultado de la acción de las mareas y del viento (Harris & Davy 1987; Miles & Davy 1993). Otros factores severos de "stress" se deben a la exposición de las raíces por la erosión por viento,

los daños por aspersion salina, ráfagas de arena, la herbivoría y las actividades humanas (Barbour et al. 1985; Maun 1994).

En este contexto ambiental se deben de considerar las características fisiológicas y la historia de vida de las plantas que se distribuyen en los ecosistemas de dunas costeras.

2.3) Las plantas pioneras de las dunas costeras

La mayor parte de las plantas que colonizan las playas son especies perennes, clonales, iteróparas con crecimiento estolonífero o rizomatoso. Estas características se encuentran entre las que propone Thompson (1987) para especies que se distribuyen en medios pobres en nutrimentos. Entre estos se encuentran muchos de los pastos que pueden encontrarse también en dunas embrionarias o principales. En los trópicos y subtrópicos, se pueden encontrar herbáceas rastreras o arbustos bajos (Moreno-Casasola et al. 1982; Moreno-Casasola & Espejel 1986; Moreno-Casasola 1988).

Respecto a la deficiencia extrema de nutrimentos de las dunas costeras, Maun (1994) ha mencionado que las plantas pueden presentar estrategias tanto de escape como de tolerancia para sobrevivir a este tipo de "stress" y menciona tres respuestas adaptativas que podrían favorecer el establecimiento de las plántulas en estos ecosistemas: (1) Las especies de dunas son capaces de sobrevivir y reproducirse en concentraciones muy bajas de nutrimentos esenciales; (2) Algunas especies de leguminosas pueden mostrar fijaciones sustanciales de N y (3) Los hongos micorrícicos juegan un papel clave en la nutrición de las especies de dunas.

Se tomarán como base estas predicciones para discutir algunas de las características fisiológicas del crecimiento de las especies de dunas.

2.4) Crecimiento de las plantas de dunas

Existen diferencias entre los patrones de crecimiento de las especies pioneras de sucesión primaria y las de sucesión secundaria. Las especies identificadas como colonizadoras comunes de sustratos primarios, se caracterizan por presentar tasas absolutas de crecimiento lentas, mientras que las pioneras de sucesión secundaria presentan tasas de crecimiento absoluto altas. Estas características destacan la diferencia crucial entre la sucesión primaria y secundaria, que es el contenido tan bajo de materia orgánica y por lo tanto de nitrógeno, de los suelos primarios (Miles & Walton 1993; Davy & Figueroa 1993).

Las características de plantas que provienen de ambientes pobres en nutrientes, han sido determinadas por muchos autores. Entre ellos que se encuentran Grime 1977; Chapin 1980, 1988, 1993; Shipley & Keddy 1988; Shipley & Peters 1990. Considerando que las especies tienden a asignar biomasa para maximizar la adquisición de los recursos limitantes para el crecimiento, al presentar tasas relativas de crecimiento lentas, con tasas de absorción también bajas, reducen el requerimiento de recursos y la probabilidad de agotar los existentes (Chapin 1980, 1988). Por otra parte, la baja disponibilidad de agua y nutrientes aumentaría la proporción raíz/parte aérea, incrementando así la asignación hacia la raíz (Root weight ratio, RWR). Con este patrón de asignación de biomasa, la mayor parte de las plantas muestran poca plasticidad ante los cambios de recursos, aunque algunas de las especies responden a pulsos de nutrientes impredecibles característicos de los habitats no productivos (Campbell & Grime 1989; Valverde et al. 1996).

En algunas investigaciones acerca del crecimiento de las plantas de dunas se ha reportado que requieren bajas concentraciones de macronutrientes para crecer (ej. Hawke & Maun 1988). Sin embargo, también se ha demostrado una correlación positiva entre las concentraciones de nutrientes y el crecimiento de las plantas, expresado en biomasa, altura y producción de hojas (Willis & Yemm 1961; Willis 1965; Pemadasa & Lovell 1974; Pavlik 1983; Hawke & Maun 1988; Maun & Krajnyk 1989; Valverde et al. 1996).

2.5) Efecto de las micorrizas arbusculares en el crecimiento

Una gran parte de los estudios realizados sobre fisiología de micorrizas arbusculares, se ha centrado en el beneficio que confieren en el crecimiento de las plantas hospederas (Hayman 1983; Tinker et al. 1992). Estos efectos se han atribuido al mejoramiento en la nutrición mineral, en el caso de las micorrizas arbusculares, principalmente al incremento en la captura de fósforo. También se ha observado la influencia en otros aspectos de la fisiología y bioquímica de la planta como incremento en la captura de iones de baja movilidad en el suelo como zinc y cobre, alteraciones en las relaciones hídricas, producción de hormonas, fijación de nitrógeno y resistencia a enfermedades de la raíz (Gianinazzi-Pearson & Gianinazzi 1983; Hayman 1983; Brundrette 1991).

El efecto de las micorrizas en el incremento en la tasa de crecimiento de las plantas se ha demostrado en una gran cantidad de especies, incluyendo cultivos y árboles. Se manifiesta en el aumento en el peso de la raíz y partes aéreas, producción de flores y rendimiento en la mayoría de las especies estudiadas (Schenck & Smith 1982; Koide 1988, Allen 1991).

Aunque la relación entre el desarrollo de micorrizas arbusculares y el mejoramiento del crecimiento de las plantas fue reportada desde Asai (1944), Daft & Nicolson (1969) demostraron que el desarrollo de micorrizas y su efecto en el crecimiento es mayor en suelos bajos en nutrientes.

Además de los estudios realizados acerca del efecto de las micorrizas en el crecimiento vegetativo de las plantas se han realizado algunos estudios en donde se demuestra que el incremento en la provisión de fósforo afecta directamente el éxito reproductivo de las plantas. Se ha encontrado un incremento en la producción de primordios florales (Dodd et al. 1983), número de flores, rendimiento de semillas de frijol de soya (Schenck & Smith 1982) y en el número de granos producidos por centeno y avena (Jensen

1982, 1983; Koide et al. 1988). También se ha encontrado que la colonización por hongos micorrícicos disminuye el tiempo requerido para iniciar la floración y la duración de la floración en algunas variedades de jitomate, así como un incremento en el número de semillas al incrementarse el número de inflorescencias e infrutescencias (Bryla & Koide 1990).

En los experimentos realizados en macetas en condiciones controladas de laboratorio o invernadero se ha logrado demostrar que la tasa de captura de fósforo por unidad de longitud de raíz se incrementa con la asociación micorrícica, lo cual da como resultado un incremento en la tasa de crecimiento de las plantas cuando este elemento es un recurso limitante. Sin embargo, en los experimentos realizados en condiciones naturales, los resultados son contradictorios. Aunque en algunos casos, los incrementos en crecimiento son considerables, en otros las diferencias no son significativas (McGonigle 1988). Existen muchos problemas para interpretar los resultados obtenidos en ecosistemas naturales. Esto se debe en parte, a que los fungicidas que se utilizan para los controles no sólo afectan a los hongos micorrícicos sino también a los patógenos, así como el efecto de forrajeo sobre esporas e hifas de hongos micorrícicos por animales. También se ha observado que durante ciertas etapas del ciclo de vida de la planta, la demanda de fósforo puede ser muy baja, por lo que la facilidad para la captura de fósforo solamente sería requerida en ciertas etapas, como por ejemplo, la floración o el estadio de plántulas (Carey et al. 1992). Por otra parte Allen & Allen (1986) han propuesto que los efectos ventajosos de las micorrizas pueden expresarse justamente, en tiempos de "stress", y que estos eventos serían los agentes selectivos durante los cuales las micorrizas son particularmente importantes para las plantas.

2.6) Sucesión y micorrizas

Las investigaciones realizadas en diferentes ecosistemas sobre la condición micorrícica de las plantas colonizadoras, particularmente en las primeras etapas sucesionales, no han aportado un patrón consistente.

Por una parte, algunos de los estudios realizados en habitats perturbados han demostrado que durante las primeras fases de la sucesión no hay micorrizas y que la mayor parte de las plantas características de estos estadios son facultativamente o no-micorrícicas. Entre estos se encuentran los resultados de Stahl (1900), Dominik (1951), Reeves et al. (1979); Miller (1979); Janos (1980).

Stahl (1900) observó que muchas de las plantas malezoides, como las Chenopodiáceas y las Brassicáceas, no eran micotróficas, pero que eran reemplazadas por plantas micotróficas. Estudiando especies de dunas costeras, Dominik (1951) reportó que las especies de sucesión temprana tendían a presentar plantas no-micorrícicas. Conforme procedía el desarrollo del suelo y se incrementaba el contenido de materia orgánica, la actividad micorrícica crecía. También Nicolson (1960) realizó estudios en dunas y observó que las plantas que se encontraban más cercanas al mar eran no-micotróficas (como por ejemplo Salsola kali). Conforme se procedía tierra adentro, tanto la asociación micorrícica como el número de esporas tendía a incrementarse y a volverse más diverso (Nicolson 1960; Nicolson & Johnston 1979). Por su parte, Reeves et al. (1979) y Miller (1979), encontraron que el potencial de inóculo en zonas áridas perturbadas por el hombre era considerablemente menor que en zonas adyacentes que no se habían alterado. Por lo tanto las plantas colonizadoras de sitios perturbados eran no-micorrícicas, mientras que las micotróficas ocupaban los sitios no-perturbados.

Janos (1980), a partir de trabajos realizados en el trópico, también determinó que la actividad micorrícica estaba ausente después de la perturbación y propuso un modelo en el que sugiere que la actividad micorrícica se incrementa durante la sucesión, asociada con los

cambios en la vegetación, de plantas no-micorrícicas a plantas facultativamente micorrícicas a plantas obligadamente micorrícicas.

A partir de estudios realizados en minas se ha demostrado que los procesos de perturbación tienden a eliminar o a reducir severamente la actividad micorrícica, ya que la infectividad de los propágulos de hongos micorrícicos arbusculares se reduce con la perturbación del suelo (Daft & Hacsckaylo 1976). Parece ser que esto se debe a la ruptura de la red de hifas en pequeños fragmentos que pierden su efectividad de inoculación (Jasper et al. 1989).

En otros estudios se ha demostrado que los estadios serales tempranos están colonizados tanto por plantas micorrícicas como no-micorrícicas. En estos se pueden incluir el trabajo de Pendleton & Smith (1983) en el Oeste de los Estados Unidos, los que se llevaron a cabo con las plantas que invadieron el volcán Santa Elena después de la erupción (Allen et al. 1984b, Allen 1987, 1988) y los de Schmidt & Scow (1986) y Hendrix & Smith (1986) en la flora de las Islas Galápagos.

Por otra parte, en algunas investigaciones realizadas en sistemas de dunas y zonas volcánicas, se ha sugerido que el desarrollo de las asociaciones micorrícicas puede ser crucial para el establecimiento de estas plantas desde las etapas más tempranas de la sucesión. Entre estas se encuentran los mayores porcentajes de sobrevivencia de *Ammophila breviligulata* en presencia de micorrizas en las dunas del Noreste de América (Koske & Polson 1984) y los altos porcentajes de especies micorrícicas que se han encontrado desde las líneas de mareas en las dunas costeras y volcanes de Hawaii (Gemma & Koske 1992).

Con base en estos resultados, Allen & Allen (1990) plantearon la hipótesis de que la condición micorrícica en la sucesión varía de acuerdo con los contenidos de humedad y nutrimentos del suelo.

FALTA

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Bibliografia

- Allen EB, Allen MF (1980) Natural re-establishment of vesicular-arbuscular mycorrhizae following stripmine reclamation in Wyoming. *J Appl Ecol* 17:139-147
- Allen, E.B. & M. F. Allen (1986) Water relations of xeric grasses in the field: Interactions of mycorrhizae and competition. *New Phytologist* 104:559-571.
- Allen EB, Allen MF (1990) The mediation of competition by mycorrhizae in successional and patchy environments. In: Grace JB, Tilman GD (eds) *Perspectives on plant competition*. Academic Press, New York, pp:367-389
- Allen MF (1987) Re-establishment of mycorrhizas on Mount-St Helens: migration vectors. *Trans Br Mycol Soc* 88:413-417
- Allen MF (1988) Re-establishment VA of mycorrhizae following severe disturbance: Comparative patch dynamics of a shrub desert and a subalpine volcano. *Proc Roy Soc Edinburgh* 94B:63-71
- Allen MF (1991) *The ecology of mycorrhizae*. Cambridge University Press
- Allen MF, MacMahon JA, Andersen DC (1984) Reestablishment of Endogonaceae on Mount St Helens: Survival of residuals. *Mycologia* 76:1031-1038
- Asai T (1934) Über das Vorkommen und die Bedeutung der Wurzel-pilze in den Landpflanzen. *Jap J Bot* 7:107-150
- Atkinson D (1973) Observations on the phosphorus nutrition of two sand dune communities at Ross Links. *J Ecol* 61:117-133
- Barbour MG, De Jong TM, Pavlick BM (1985) Marine beach and dune plant communities. In: Chabot BF, Mooney HA (eds) *Physiological ecology of North American plant communities*. Chapman and Hall, New York, London, pp 297-322
- Boorman LA (1982) Some plant growth patterns in relation to the sand dune habitat. *J Ecol* 70:607-614

- Brundrett M (1991). Mycorrhizas in natural ecosystems. *Advances in ecological research* 21:171
- Bryla DR, Koide TR (1990). Regulation of reproduction in wild and cultivated *Lycopersicon esculentum* Mill. by vesicular-arbuscular mycorrhizal infection. *Oecologia* 84:74-81.
- Campbell BD, Grime JP (1989) A comparative study of plants responsiveness to the duration of episodes of mineral nutrient enrichment. *New Phytol* 112:261-267
- Carey PD, Fitter AH, Watkinson AR (1992) A field study using the fungicide benomyl to investigate the effect of mycorrhizal fungi on plant fitness. *Oecologia*
- Chapin FS (1980) The mineral nutrition of wild plants. *Ann Rev Ecol Syst* 11:233-260
- Chapin FS (1988) Ecological aspects of plant mineral nutrition. *Adv Min Nut* 3:161-191
- Chapin FS (1993) Physiological controls over plant establishment in primary succession. In: Miles J, Walton DWH (eds) *Primary succession on land*. Blackwell Scientific Publications, Oxford, pp:161-178
- Chapman VJ (1976) *Coastal Vegetation*. Pergamon Press, Oxford
- Clough KS, Sutton JC (1978) Direct observation of fungal aggregates in sand dune soil. *Can J Microbiol* 24:333-335
- Cowles HC 1899 The ecological relations of the vegetation on the sand dunes of Lake Michigan. *Bot Gaz* 27:95-117
- Daft MJ, Nicolson TH (1969) Effect of Endogone mycorrhizae on plant growth. III. Influence of inoculum concentration on growth and infection in tomato. *New Phytol* 68:933-963
- Daft MJ, Nicolson TH (1974) Arbuscular mycorrhizas in plants colonizing coal wastes in Scotland. *New Phytol* 73:1129-1138
- Daft MJ, Hacskeylo E (1976) Arbuscular mycorrhizas in anthracite and bituminous coal wastes of Pennsylvania. *J Appl Ecol* 13:523-531

- Davy AJ, Figueroa ME (1993) The colonization of strandlines. In: Miles J, Walton DWH (eds) Primary succession on land. Blackwell Scientific Publications, Oxford, pp:113-131
- Dodd J, Krikun J, Haas J (1983) Relative effectiveness of indigenous populations of vesicular-arbuscular mycorrhizal fungi from four sites in the Negev. *Israel J Bot* 32:10-21
- Doing H (1985) Coastal fore-dune zonation and succession in various parts of the world. *Vegetatio* 61:65-75
- Dominik T (1951) Badania mykotrofizmu roslinnosci wydm nadmorskich i srodladowyck. *Acta Soc Bot Pol* 21:125-164
- Ehrenfeld JG (1990) Dynamics and processes of barrier island vegetation. *Aquatic Sci* 2:437-480
- Forster SM (1979) Microbial aggregation of sand in an embryo dune system. *Soil Biol Biochem* 11:537-543
- Forster SM, Nicolson TH (1981a) Microbial aggregation of sand in a maritime dune succession. *Soil Biol Biochem* 13:205-208
- Forster SM, Nicolson TH (1981b) Aggregation of sand from a maritime embryo sand dune by microorganisms and higher plants. *Soil Biol Biochem* 13:199-203
- Gemma JN, Koske RE (1988) Seasonal variation in spore abundance and dormancy of Gigaspora gigantea and in mycorrhizal inoculum potential of a dune soil. *Mycologia* 80:211-216
- Gemma JN, Koske RE (1989) Field inoculation of American beachgrass (Ammophila breviligulata) with V-A mycorrhizal fungi. *J Environ Manag* 29:173-182
- Gemma JN, Koske RE (1992) Are mycorrhizal fungi present in the early stages of primary succession. In: Read DJ, Lewis DH, Fitter AH, Alexander IJ (eds) *Mycorrhizas in ecosystems*, CAB international, University Press, Cambridge, pp 183-189

- Gemma JN, Koske RE, Carreiro M (1989) Seasonal dynamics of selected species of V-A mycorrhizal fungi in a sand dune. *Mycol Res* 92:317-321
- Gianinazzi-Pearson V, Gianinazzi S (1983) The physiology of vesicular-arbuscular mycorrhizal roots. *Plant and Soil* 71:197-209.
- Giovannetti M (1985) Seasonal variations of vesicular-arbuscular mycorrhizas and Endogonaceous spores in a maritime sand dune. *Trans Br Mycol Soc* 84:679-684
- Giovannetti M, Nicolson TH (1983) Vesicular-arbuscular mycorrhizas in Italian sand dunes. *Trans Br Mycol Soc* 80:552-557
- Grime JP (1977) Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *Am Nat* 111:1169-1194
- Harley, J. L. & S. E. Smith (1983). *Mycorrhizal Symbiosis*. Academic Press, London.
- Harris D, Davy AJ (1987) Seedling growth in *Elymus farctus* after Episodes of burial with sand. *Ann Bot* 60:587-593
- Hayman DS (1983) The physiology of vesicular-arbuscular endomycorrhizal symbiosis. *Can J Bot* 61:944-963.
- Hawke MA, Maun MA (1988) Some aspects of nitrogen, phosphorus, and potassium nutrition of three colonizing beach species. *Can J Bot* 66:1490-1496
- Huang RS, Smith WK, Yost R (1985) Influence of vesicular-arbuscular mycorrhizae on growth, water relations, and leaf orientation in *Leucaena leucocephala* (Lam) de Wit. *New Phytologist* 99:229-244.
- Janos DP (1980) Mycorrhizae influence tropical succession. *Biotropica* 12:56-64
- Jasper DA, Abbot LK, Robson AD (1989) Soil disturbance reduces infectivity of external hyphae of vesicular arbuscular mycorrhizal fungi. *New Phytol* 112:93-99
- Jehne W, Thompson CH (1981) Endomycorrhizae in plant colonization on coastal sand dunes at Cooloola, Queensland. *Aust J Ecol* 6:221-230
- Jensen A (1982) Influence of four vesicular-arbuscular mycorrhizal fungi on nutrient uptake and growth in barley (*Hordeum vulgare*). *New Phytol* 90:45-50

- Jensen A (1983) The effect of indigenous vesicular-arbuscular mycorrhizal fungi on nutrient uptake and growth of barley in two Danish soils. *Plant Soil* 70:155-163
- Kellman M, Roulet N (1990) Nutrient flux and retention in a tropical sand-dune succession. *J Ecol* 78:664-676
- Kendrick (1991) Fungal Symbioses and Evolutionary Innovations. In: Margulis L, Fester R (eds). *Symbiosis as a source of Evolutionary Innovation in Speciation and Morphogenesis*. Massachusetts Institute of Technology Press, Cambridge. pp. 249-261
- Koide RT, Li M, Lewis J, Irby C (1988) Role of mycorrhizal infection in the growth and reproduction of wild vs. cultivated plants. *Oecologia* 77:537-543
- Koske RE (1988) Vesicular-Arbuscular mycorrhizae of some Hawaiian dune plants. *Pacific Sci* 42:217-229
- Koske RE, Sutton JC, Sheppard BR (1975) Ecology of Endogone in Lake Huron sand dunes. *Can J Bot* 53:87-93
- Koske RE, Halvorson WL (1981) Ecological studies of vesicular-arbuscular mycorrhizae in a barrier sand dune. *Can J Bot* 59:1413-1422
- Koske RE, Polson WR (1984) Are VA mycorrhizae required for sand dune stabilization? *Bioscience* 34:420-424
- Koske RE, Halvorson WL (1989) Mycorrhizal associations of selected plant species from San Miguel Island, Channel Islands National Park, California. *Pacific Sci* 43:32-40
- Koske RE, Gemma JN (1990) VA mycorrhizae in strand vegetation of Hawaii: Evidence for long distance codispersal of plants and fungi. *Amer J Bot* 77:466-474
- Logan VS, Clarke PJ, Allaway WG (1989) Mycorrhizas and root attributes of plants of coastal sand-dunes of New South Wales. *Aust J Plant Physiol* 16:141-146
- Louis I (1990) A mycorrhizal survey of plant species colonizing coastal reclaimed land in Singapore. *Mycologia* 82:772-778
- McGonigle, T. P. & A. H. Fitter (1988). Ecological consequences of arthropod grazing on VA mycorrhizal fungi. *Proceedings of the Royal Society of Edinburgh* 94B:25-32.

- Martínez ML, Moreno-Casasola P, Castillo S (1993) Biodiversidad Costera: Playas y dunas. In: Salazar-Vallejo SI, González NE (eds) Biodiversidad marina y costera de México, Com Nal Biodiversidad y CIQRO, México, pp 160-181
- Maun MA (1985) Population biology of Ammophila breviligulata and Calamovilfa longifolia on Lake Huron sand dunes I. Habitat, growth form, reproduction and establishment. *Can J Bot* 43:113-124
- Maun MA (1994) Adaptations enhancing survival and establishment of seedlings on coastal dune systems. *Vegetatio* 111:59-70
- Miles & Walton (1993) Primary succession revisited. In: Miles J, Walton DWH (eds) Primary succession on land. Blackwell Scientific Publications, Oxford, pp: 295-302.
- Miller RM (1979) Some occurrences of vesicular-arbuscular mycorrhizae in natural and disturbed ecosystems of the Red Desert. *Can J Bot* 57:619-623
- Mc Gonigle TP (1988) A numerical analysis of published field trials with vesicular-arbuscular mycorrhizal fungi. *Funct Ecol*
- Moreno-Casasola P (1982) Ecología de la vegetación de dunas costeras: Factores físicos. *Biotica* 7:577-602
- Moreno-Casasola P (1986) Sand movement as a factor in the distribution of plant communities in a coastal dune system. *Vegetatio* 65:67-76
- Moreno-Casasola P (1988) Patterns of plant species distribution on coastal dunes along the Gulf of Mexico. *J Biogeogr* 15:787-806
- Moreno-Casasola P, van der Maarel E, Castillo S, Huesca ML, Pisanty I (1982) Ecología de la vegetación de dunas costeras: Estructura y composición en el Morro de la Mancha, Ver. *Biotica* 7:491-526
- Moreno-Casasola P and Espejel I (1986) Classification and ordination of coastal sand dune vegetation along the Gulf and Caribbean sea of Mexico. *Vegetatio* 66:147-182
- Nicolson TH (1960) Mycorrhizae in the Gramineae, II. Development in different habitats particularly sand dunes. *Trans Br Mycol Soc* 43:132-145

- Nicolson TH, Johnston C (1979) Mycorrhiza in the Gramineae III. Glomus fasciculatus as the endophyte of pioneer grasses in a maritime sand dune. *Trans Br Mycol Soc* 72:262-268
- Old KM, Nicolson TH (1975) Electron microscopical studies of the microflora of roots of sand dune grasses. *New Phytol* 74:51-58
- Pavlik BM (1983) Nutrient and productivity relations of the dune grasses Ammophila arenaria and Elymus farctus. II. Growth and patterns of dry matter and nitrogen allocation as influenced by nitrogen supply. *Oecologia* 57:233-238
- Pemadasa MA, Lovell PH (1974) The mineral nutrition of some dune annuals. *J Ecol* 62:647-657
- Pendleton RL, Smith BN (1983) Vesicular-arbuscular mycorrhizae of weedy and colonizer plant species at disturbed sites in Utah. *Oecologia (Berl)* 59:296-301
- Peterson RL, Ashford AE, Allaway G (1985) Vesicular-arbuscular mycorrhizal associations of vascular plants on Heron Island. A greater barrier coral cay. *Aust J Bot* 33:669-676
- Puppi G (1982) L'uso delle micorrizze vescicolari-arbuscolari nel recupero di terreno sabbiosi, erosi, di discarica e di miniera. *Mic. Ital.* 2:5-10
- Puppi G, Tabacchini P, Riess S, Sanvito A (1986) Seasonal patterns in mycorrhizal association in a maritime sand dune system. In: Gianninazzi-Pearson V, Gianninazzi S (eds) *Physiological and genetical aspects of mycorrhizae*, Paris, INRA pp 245-251
- Puppi G, Chiapperi F, Tabacchini P, Sanvito A, Carpigo F (1986) Endogonaceae del litorale tirrenico. *Mic. Ital.* 2:7-14
- Puppi G, Riess S (1987) Role and ecology of VA mycorrhizae in sand dunes. *Angew Botanik* 61:115-126
- Ranwell D (1972) *Ecology of salt marshes and sand dunes*. Chapman and Hall, London
- Read DJ (1989) Mycorrhizas and nutrient cycling in sand dune ecosystems. *Proc Roy Soc Edinburgh* 96B:89-100

- Reeves FB, Wagner DW, Moorman T, Kiel J (1979) The role of endomycorrhizae in revegetation practices in the semi-arid west. I. A comparison of incidence of mycorrhizae in severely disturbed vs. natural environments. *Amer J Bot* 66: 1-13
- Salas M (1994) Efecto de las micorrizas vesículo-arbusculares en la competencia por nutrimentos entre dos especies pioneras de dunas costeras del Morro de la Mancha, Veracruz. B Sc Thesis, UNAM, Mexico
- Sanders IR, Fitter AH (1992) The ecology and functioning of vesicular-arbuscular mycorrhizas in co-existing grassland species. I. seasonal patterns of mycorrhizal occurrence and morphology. *New Phytol* 120:517-524
- Schmidt SK, Scow KM (1986) Mycorrhizal fungi on the Galapagos Islands. *Biotropica* 18:236-240
- Shipley B, Keddy PA (1988) The relationship between relative growth rate and sensitivity to nutrient stress in twenty-eight species of emergent macrophytes. *J Ecol* 76:1101-1110
- Shipley B, Peters RH (1990) The allometry of seed weight and seedling relative growth rate. *Funct Ecol* 4:523-529
- Stahl E (1900) Der Sinn der Mycorrhizenbildung. Eine vergleichend-biologische Studie. *Jahrbuch für Wissenschaftliche Botanik* 34:539-668
- Sutton JC, Sheppard BR (1976) Aggregation of sand dune soil by endomycorrhizal fungi. *Can J Bot* 54:326-333
- Sylvia DM (1986) Spatial and temporal distribution of vesicular-arbuscular mycorrhizal fungi associated with Uniola paniculata in Florida foredunes. *Mycologia* 78:728-734
- Sylvia DM, Burks JN (1988) Selection of a vesicular arbuscular mycorrhizal fungus for practical inoculation of Uniola paniculata. *Mycologia* 80:565-568
- Tinker PB, Jones MD, Durall DM (1992) A functional comparison of Ecto and Endomycorrhizas. In: Read DJ, Lewis DH, Fitter AH, Alexander IJ (eds). *Mycorrhizas in ecosystems*, CAB International. pp.303-310

- Valverde T (1992) Historia de vida de *Schyzachirium scoparium* var. *littoralis* en diferentes microambientes de dunas costeras. MSc Thesis. Facultad de Ciencias, UNAM, Mexico
- Valverde T, Pisanty I, Rincón E (en prensa) Growth responses of six tropical dune plant species to different nutrient regimes. *J Coastal Res*
- Webley DM, Eastwood DJ, Gimingham CH (1952) Development of a soil microflora in relation to plant succession on sand-dunes, including the rhizosphere flora associated with colonizing species. *J Ecol* 40:168-178
- Willis AJ (1965) The influence of mineral nutrients on the growth of *Ammophila Arenaria*. *J Ecol* 735-745
- Willis AJ, Folkes BF, Hope-Simon JF, Yemm EW (1959) Braunton Burrows: The dune system and its vegetation. *J Ecol* 47:1-24
- Willis AJ, Yemm EW (1961) Braunton Burrows: Mineral nutrient status of the dune soils. *J Ecol* 49:377-390

2.7) Arbuscular mycorrhizae in coastal sand dune ecosystems

At the beginnings of the XXth century, plants from sand dune ecosystems were reported to be associated to arbuscular mycorrhizal fungi (AMF), when Stahl (1900) observed the presence of mycorrhizal structures in Panicum maritima, Convolvulus soldanella and Cineraria maritima in the coasts of Liguria, in Italy, and Asai (1934) in some plants from Japanese coastal dunes. Since then, many studies have been conducted in different places throughout the world (Fig. 1).

In the 50's, Dominik (1951) mentioned that nonmycorrhizal plants were present in the early successional coastal sand dunes, but that mycorrhizal activity increased with soil development and organic matter. A close relationship between the soil microflora (bacteria and fungi) and plant succession was also found in a sand dune ecosystem in Scotland (Webley et al. 1952), so it was suggested that the microflora contributed to the stabilization of these ecosystems. However, the first experimental evidence, particularly for mycorrhizal fungi, was not provided until the 60's, when the publication of the first study on mycorrhizal status of sand dune species in different successional stages appeared (Nicolson 1960). Examination of root samples from sand dunes in Scotland, indicated that the degree of AMF colonization varied with respect to the succession of vegetation, increasing from the foredunes to recently fixed dunes (Nicolson 1960). Further evidences were provided later. Around the 70's, the studies of Koske et al. (1975), Old & Nicolson (1975), Sutton & Sheppard (1976), Clough & Sutton (1978), Forster (1979), Forster & Nicolson (1981a, b), Jehne & Thompson (1981) and more recently of Rose (1988), demonstrated that the external mycelium of VAM fungi plays a significant role in the process of dune stabilization. In some experiments it was observed that the roots alone had little effect on aggregation (Koske et al. 1975; Sutton & Sheppard 1976; Forster & Nicolson 1981b), and that sand grains are bound together mechanically by the AMF hyphae (Koske et al. 1975; Clough & Sutton 1978; Forster & Nicolson 1981a). It was also reported that the amounts of

external mycelium and aggregates increased as the dunes became stable and higher plant succession developed (Forster & Nicolson 1981a; Rose 1988). As Forster & Nicolson (1981b) stated: "Aggregates are more resistant to wind erosion, increase the moisture content and nutrient status of sand, which allows further colonization by higher plants leading to sand stabilization".

Up to the 90's, most of the investigations contributed mainly with studies on the fungal partner of the symbiosis. The main objectives were to identify the arbuscular mycorrhizal fungi which colonized the roots of the dune species (Table 1), to find their patterns of distribution and abundance, as well as to determine the sand dune plants to which they were associated. All the studies on the arrangement of AMF spores in the natural ecosystems showed an aggregated type of distribution (Koske & Halvorson 1981; Giovannetti 1985; Sylvia 1986; Tews & Koske 1986; St. John & Koske 1988; Koske & Gemma 1989). Most of the results obtained supported the spatial pattern of spore abundance and infection percentage found by Nicolson (1960) (e.g. Koske & Polson 1984; Louis 1990). In addition, a seasonal pattern in the numbers of spores and colonization percentage was also found, mainly in the temperate ecosystems. Studies of different dune systems in Scotland (Nicolson & Johnston 1979), Italy (Giovannetti 1985; Puppi & Riess 1987) and San Miguel Island in US (Koske & Halvorson 1989a), among others, demonstrated that the values of AMF colonization vary in different seasons. Some studies showed higher spore abundance at the end of the growing season (Giovannetti 1985), while others reported that although all the population of AMF spores increases as plants mature, individual species behave differently. For example, in Florida sand dunes, three species were more abundant in August and two in November (Sylvia 1986). Antagonistic interactions between species have also been suggested. High spore abundance by one species being associated with low abundance of another one (Gemma et al. 1989). Spore abundance could also be determining the species colonized, as shown in some annual

species, where lack of infection seems to be related to the low spore availability in their growth cycle (Ernst et al. 1984).

Throughout this period, all the surveys on mycorrhizal status demonstrated that most of the species which are distributed in sand dunes were heavily colonized by arbuscular mycorrhizal fungi (Giovannetti & Nicolson 1983; Peterson et al. 1985; Koske & Halvorson 1989b; Logan et al. 1989; Koske & Gemma 1990), even some members of reported non-mycorrhizal families (Logan et al. 1989).

In addition to the studies being conducted on taxonomy and distribution of AMF spores (Abe et al. 1994, 1995; Stürmer & Bellei 1994; Koske & Gemma, submitted), other recent investigations have been directed towards the role of mycorrhizae in survival, establishment and growth of sand dune species (Sylvia & Burks 1989; Will & Sylvia 1990; Koske & Gemma 1995; Gemma & Koske submitted). The results obtained indicate that mycorrhizal association does not benefit all the species (Koske & Gemma 1995; Gemma & Koske submitted). The studies conducted about the effect of mycorrhizae in the survival and growth of Ammophila breviligulata, have shown increased survival and growth (Nicolson & Johnston 1979; Koske & Polson 1984), as well as an improvement in the establishment, a more vigorous early growth and a greater panicle production of the field-inoculated plants in contrast to the uninoculated ones (Gemma & Koske 1989; Gemma & Koske submitted). It has also been demonstrated that AMF improved the relative growth rate and root dry weight of buried plants infected with nematodes (Little & Maun, submitted).

All these studies support the role of mycorrhizae in sand dune stabilization and are strongly suggesting their importance in the management and conservation of these ecosystems (Will & Sylvia 1990; Koske & Gemma 1995). The results obtained are even questioning the role of mycorrhizae in primary succession.



Fig. 1 Distribution of research on mycorrhizae in coastal sand dune ecosystems

Fig. 1. Distribution of research on mycorrhizae in coastal sand dune ecosystems.

CANADA

Lake Huron

- 1) Koske et al. 1975
- 2) Sutton and Sheppard 1976
- 3) Clough and Sutton 1978
- 4) Little and Maun, submitted

Quebec, New Brunswick, Nova Scotia

- 5) Dalpé 1989

UNITED STATES OF AMERICA

Wisconsin

- 6) Koske and Tews 1987

Great Basin, Colorado

- 7) Al-Agely and Reeves 1995

Massachusetts

- 8) Bergen and Koske 1984
- 9) Gemma and Koske 1989
- 10) Gemma et al. 1989
- 11) Allen and Allen 1992
- 12) Gemma and Koske 1992
- 13) Koske and Gemma, submitted
- 14) Gemma and Koske, submitted

Rhode Island

- 15) Koske 1981a
- 16) Koske 1981b
- 17) Koske and Halvorson 1981
- 18) Koske 1982a
- 19) Koske 1982b
- 20) Koske et al. 1983
- 21) Koske and Walker 1984
- 22) Koske 1986
- 23) Koske et al. 1986
- 24) Gemma and Koske 1988a
- 25) Gemma and Koske 1988b
- 26) Friese and Koske 1991

New Jersey to Virginia

- 27) Koske 1987

Georgia to Maine

- 28) Koske and Polson 1984

Florida

- 29) Sylvia 1986
- 30) Sylvia and Will 1988
- 31) Sylvia and Burks 1988
- 32) Sylvia 1989
- 33) Will and Sylvia 1990
- 34) Sylvia et al. 1993

California

- 35) Halvorson and Koske 1987
- 36) Koske and Halvorson 1989a
- 37) Koske and Halvorson 1989b
- 38) Rose 1988

Hawaii

- 39) Koske et al. 1986
- 40) Koske 1988
- 41) Koske and Gemma 1989
- 42) Koske and Gemma 1990
- 43) Gemma and Koske 1992
- 44) Koske and Gemma 1995a
- 45) Koske and Gemma 1995b
- 46) Koske and Gemma 1996

MEXICO

- 47) Sigüenza et al. 1996
- 48) Corkidi and Rincón (submitted)

BRAZIL

- 49) Stürmer and Bellei 1994

SCOTLAND

- 50) Nicolson 1959
- 51) Nicolson 1960
- 52) Old and Nicolson 1975
- 53) Forster 1979
- 54) Nicolson and Johnston 1979
- 55) Forster and Nicolson 1981a
- 56) Forster and Nicolson 1981b

ENGLAND

- 57) Harley and Harley 1987

HOLLAND

- 58) Ernst et al. 1984

POLAND

- 59) Blaszkowski 1994

ITALY

- 60) Stahl 1900
- 61) Puppi 1982
- 62) Giovannetti and Nicolson 1983
- 63) Giovannetti 1985
- 64) Pacioni et al. 1985
- 65) Puppi et al. 1986 a, b
- 66) Puppi and Riess 1987
- 67) Pacioni and Puppi 1988

PAKISTAN

68) Khan 1974

INDIA

69) Mohankumar et al. 1988

SINGAPORE

70) Louis 1990

MALAYSIA

71) Chulan et al. 1983

JAPAN

72) Asai 1934

73) Abe et al. 1994

74) Abe and Katsuya 1995

A U S T R A L I A

75) Koske 1975

76) Jehne and Thompson 1981

77) Peterson et al. 1985

78) Logan et al. 1989

<i>Glomus trimurales</i> Koske & Halvorson						SM								
<i>Sclerocystis rubiformis</i> Gerdemann & Trappe	CA													
<i>Sclerocystis sinuosa</i> Gerd. & Bakshi							HA							
<i>Scutellospora arenicola</i> Koske & Halvorson						SM								
<i>Scutellospora calospora</i> (Nicol. & Gerd.) Walker & Sanders	CA	WI	MA	RHI	NV	SM		IT		P	AU			
<i>Scutellospora coralloidea</i> (Trappe, Gerd. & Ho) Walker & Sanders								BR						
<i>Scutellospora dipapillosa</i> (Walker & Koske) Walker & Sanders		WI		RHI	NV									
<i>Scutellospora dipurpurascens</i> Morton & Koske										P				
<i>Scutellospora erythropha</i> (Koske & Walker) Walker & Sanders			MA	RHI	NV									
<i>Scutellospora fulgida</i> Koske & Walker					NV									
<i>Scutellospora gregaria</i> (Schenck & Nicolson) Walker & Sanders								BR	IT					JAP
<i>Scutellospora heterogama</i> (Nicol. & Gerd.) Walker & Sanders									IT					
<i>Scutellospora nodosa</i> Blaszcz.											P			
<i>Scutellospora pellucida</i> (Nicol. & Schenck) Walker & Sanders	CA		MA	RHI	NV						P			
<i>Scutellospora persica</i> (Koske & Walker) Walker & Sanders			MA	RHI	NV				IT					
<i>Scutellospora reticulata</i> (Koske, Miller & Walker) Walker & Sanders				RHI										
<i>Scutellospora scutata</i> Walker & Dierderichs								BR						
<i>Scutellospora verrucosa</i> Koske & Walker					NV	FI								
<i>Scutellospora weresubiae</i> Koske & Walker					NV	FI		BR						

References

- Abe JP, Masuhara G, Katsuya K (1994) Vesicular-arbuscular mycorrhizal fungi in coastal dune plant communities I. Spore formation of *Glomus* spp. predominates under a patch of *Elymus mollis*. *Mycoscience* 35:233-238
- Abe JP, Katsuya K (1995) Vesicular-arbuscular mycorrhizal fungi in coastal dune plant communities II. Spore formation of *Glomus* spp. predominates under geographically separated patches of *Elymus mollis*. *Mycoscience* 36:113-116
- Al-Agely AK, Reeves FB (1995) Inland sand dune mycorrhizae: Effects of soil depth, moisture, and pH on colonization of *Oryzopsis hymenoides*. *Mycologia* 87:54-60
- Allen MF, Allen EB (1992) Mycorrhizae and plant community development: mechanisms and patterns. In: Carrol JC, Wicklow DT (eds) *The fungal community: its organization and role in the ecosystem*. Dekker, New York, pp 455-479
- Asai T (1934) Uber das Vorkommen und die Bedeutung der Wurzel-pilze in den Landpflanzen. *Jap J Bot* 7:107-150
- Bergen M, Koske RE (1984) Vesicular-arbuscular mycorrhizal fungi from Sand Dunes of Cape Cod, Massachusetts. *Trans Br Mycol Soc* 83:157-158
- Blaszkowski J (1994) Arbuscular fungi and mycorrhizae (Glomales) of the Hel Peninsula, Poland. *Mycorrhiza* 5:71-88
- Chulan A, Yaacob O, Kamal AJM, Paramanathan S (1983) Distribution of VA mycorrhizal spores in sandy beach soils under cashew. *Pertanika* 6:15-20
- Clough, KS, Sutton JC (1978) Direct observation of fungal aggregates in sand dune soil. *Canadian J Microbiol* 24:333-335
- Dalpé Y (1989) Inventaire et répartition de la flore endomycorrhizienne de dunes et de rivages maritimes du Québec, du Nouveau Brunswick et de la Nouvelle-Ecosse. *Nat Can* 116:219-236
- Dominik T (1951) Badania mykotrofizmu roslinnosci wydm nadmorskich i srodladowyck. *Acta Soc Bot Pol* 21:125-164

- Ernst WHO, Van Duin WE, Oolbekking GT (1984) Vesicular-arbuscular mycorrhiza in dune vegetation. *Acta Bot Neerl* 33:151-160
- Forster SM (1979) Microbial aggregation of sand in an Embryo dune system. *Soil Biol Biochem* 11:537-543
- Forster SM, Nicolson TH (1981a) Microbial aggregation of sand in a maritime dune succession. *Soil Biol Biochem* 13:205-208
- Forster SM, Nicolson TH (1981b) Aggregation of Sand from a Maritime Embryo sand Dune by microorganisms and higher plants. *Soil Biol Biochem* 13:199-203
- Francis R, Read DJ (1995) Mutualism and antagonism in the mycorrhizal symbiosis, with special reference to impacts on plant community structure. *Can J Bot* 73:S1301-S1309
- Friese CR, Koske RE (1991) The spatial dispersion of spores of vesicular-arbuscular mycorrhizal fungi in a sand dune: Microscale patterns associated with the root architecture of individual American beachgrass. *Mycol Res* 95:952-957
- Gemma JN, Koske RE (1988a) Seasonal Variation in spore abundance and dormancy of Gigaspora gigantea and in mycorrhizal inoculum potential of a dune soil. *Mycologia* 80:211-216
- Gemma JN, Koske RE (1988b) Pre-infection interactions between roots and the mycorrhizal fungus Gigaspora gigantea: Chemotropism of germ-tubes and root growth response. *Trans Brit Mycol Soc* 91:123-132
- Gemma JN, Koske RE (1989) Field inoculation of American Beachgrass (Ammophila breviligulata) with V-A mycorrhizal fungi. *J Environ Manag* 29:173-182
- Gemma JN, Koske RE, Carreiro M (1989) Seasonal dynamics of selected species of V-A mycorrhizal fungi in a sand dune. *Mycol Res* 92:317-321

- Gemma JN, Koske RE (1992) Are mycorrhizal fungi present in the early stages of primary succession. In: Read DJ, Lewis DH, Fitter AH, Alexander IJ (eds) *Mycorrhizas in ecosystems*, CAB international, University Press, Cambridge, pp 183-189
- Gemma JN, Koske RE (submitted) Arbuscular mycorrhizae in coastal sand dune plants: Field and greenhouse inoculation and presence of mycorrhizae in planting stock.
- Giovannetti M (1985) Seasonal variations of Vesicular-Arbuscular Mycorrhizas and Endogonaceous Spores in a maritime sand dune. *Trans Brit Mycol Soc* 84:679-684
- Giovannetti M, Nicolson TH (1983) Vesicular-arbuscular mycorrhizas in Italian Sand dunes. *Trans Brit Mycol Soc* 80: 552-557
- Halvorson WL, Koske RE (1987) Mycorrhizae associated with an invasion of Erechtites glomerata (Asteraceae) on San Miguel Island, California. *Madroño* 34:260-268
- Harley JL, Harley EL (1987) A check-list of mycorrhizae in the British flora. *New Phytol* 105:1-102
- Jehne W, Thompson CH (1981) Endomycorrhizae in plant colonization on coastal sand dunes at Cooloolo, Queensland. *Aust J Ecol* 6:221-230
- Khan AG (1974) The occurrence of mycorrhizas in halophytes, hydrophytes and xerophytes, and of Endogone spores in adjacent soils. *J Gen Microbiol* 81:7-14
- Koske RE (1975) Endogone spores in Australian sand dunes. *Can J Bot* 53:668-672
- Koske RE (1981a) Multiple germination by spores of Gigaspora gigantea. *Trans Brit Mycol Soc* 76:328-330
- Koske RE (1981b) Gigaspora gigantea: Observations on spore germination of a VA-mycorrhizal fungus. *Mycologia* 73:288-300
- Koske RE (1981c) Labyrinthula inside the spores of a vesicular-arbuscular mycorrhizal fungus. *Mycologia* LXXII:1175-1180
- Koske RE (1981d) A preliminary study of interactions between species of vesicular-arbuscular fungi in a sand dune. *Trans Brit Mycol Soc* 76: 411-416

- Koske RE (1982) Evidence for a volatile attractant from plant roots affecting germ tubes of a VA mycorrhizal fungus. *Trans Brit Mycol Soc* 79: 305-310
- Koske RE (1984) Spores of VAM fungi inside spores of VAM fungi. *Mycologia* 76:853-862
- Koske RE (1986) Checklist of vesicular-arbuscular mycorrhizal fungi from maritime sand dunes of Rhode Island. *Mycol Soc Am Newsletter* 37:43
- Koske RE (1987) Distribution of VA mycorrhizal fungi along a latitudinal temperature gradient. *Mycologia* 79:55-68
- Koske RE (1988) Vesicular-Arbuscular Mycorrhizae of some Hawaiian Dune Plants. *Pacific Sci* 42:217-229
- Koske RE., Sutton JC, Sheppard BR (1975) Ecology of Endogone in Lake Huron sand dunes. *Can J Bot* 53:87-93
- Koske RE, Halvorson WL (1981) Ecological studies of vesicular-arbuscular mycorrhizae in a barrier sand dune. *Can J Bot* 59:1413-1422
- Koske RE, Doud Miller D, Walker C (1983) Gigaspora reticulata: A newley described endomycorrhizal fungus from New England. *Mycotaxon* XVI:429-435
- Koske RE, Polson WR (1984) Are VA mycorrhizae required for sand dune stabilization? *Bioscience* 34: 420-424
- Koske RE, Walker C (1984) Gigaspora erythropha, a new species forming arbuscular mycorrhizae. *Mycologia* 76(2):250-255
- Koske RE, Walker C (1985) Species of Gigaspora (Endogonaceae) with roughened outer walls. *Mycologia* 77:702-720
- Koske RE, Friese CF, Olexia PD, Hauke RL (1985) Vesicular-arbuscular mycorrhizas in Equisetum. *Trans Brit Mycol Soc* 85:350-353
- Koske RE, Friese CF, Walker C, Dalpé Y (1986a) Glomus pustulatum: A New species in the Endogonaceae. *Mycotaxon* XXVI:143-149

- Koske RE, Gemma JN, Olexia PD (1986b) Glomus microaggregatum, a new species in the Endogonaceae. Mycotaxon XXVI:125-132
- Koske RE, Walker C (1986a) Species of Scutellospora (Endogonaceae) with smooth-walled spores from maritime sand dunes: Two new species and a redescription of the spores of Scutellospora pellucida and Scutellospora calospora. Mycotaxon XXVII:219-235
- Koske RE, Walker C (1986b) Glomus globiferum: A new species of Endogonaceae with a hyphal peridium. Mycotaxon XXVI:133-142
- Koske RE, Tews LL (1987) Vesicular-arbuscular mycorrhizal fungi of Wisconsin sandy soils. Mycologia 79:901-905
- Koske RE, Gemma JN (1989) Glomus nanolumen (Endogonaceae), a new species from Hawaii. Mycologia 81:935-938
- Koske RE, Gemma JN, Mueller C (1989) Observations on sporocarps of the VA mycorrhizal fungus Rhizophagus litchii. Mycol Res 92: 488-490
- Koske RE, Halvorson WL (1989a) Scutellospora arenicola and Glomus trimurales: two new species in the Endogonaceae. Mycologia 81 (6):927-933
- Koske RE, Halvorson WL (1989b) Mycorrhizal Associations of selected plant species from San Miguel Island, Channel Islands National Park, California. Pacific Sci 43:32-40
- Koske RE, Gemma JN (1990) VA Mycorrhizae in strand vegetation of Hawaii: Evidence for long-distance codispersal of plants and fungi. Am J Bot 77:466-474
- Koske RE, Gemma JN (1995) Scutellospora hawaiiensis: A new species of arbuscular mycorrhizal fungus from Hawaii. Mycologia 87:678-683
- Koske RE, Gemma JN (1996) Arbuscular mycorrhizal fungi in Hawaiian sand dunes: Island of Kauai. Pacific Sci 50:36-45
- Little LR, Maun MA The "Ammophila problem" revisited: A role for mycorrhizal fungi
- Nicolson TH (1959) Mycorrhizae in the Gramineae, I. Vesicular-arbuscular endophytes, with special reference to the external phase. Trans Brit Mycol Soc 42:421-438

- Logan VS, Clarke PJ, Allaway WG (1989) Mycorrhizas and root attributes of plants of coastal sand dunes of New South Wales. *Aust J Plant Physiol* 16:141-146
- Mohankumar V, Ragupathy S, Nirmala CB, Mahadevan A (1988) Distribution of vesicular arbuscular mycorrhizae (VAM) in the sandy beach soils of Madras Coast. *Current Sci* 57(7):367-368
- Nicolson TH (1960) Mycorrhizae in the Gramineae. II. Development in different habitat particularly sand dunes. *Trans Brit Mycol Soc* 43: 132-145
- Nicolson TH, Johnston C (1979) Mycorrhiza in the Gramineae. III. Glomus fasciculatus as the endophyte of pioneer grasses in a maritime sand dune. *Trans Brit Mycol Soc* 72: 262-268
- Old KM, Nicolson TH (1975) Electron microscopical studies of the microflora of roots of sand dune grasses. *New Phytol* 74:51-58
- Pacioni G, La Salvia M, Rosa S, Trotta G (1985) The annual dynamic of VA-mycorrhizae in a maritime sandy dune (Central East Italy). *Proc 6th NACOM*, June 25-29, 1984, Bend, Oregon, p 286
- Pacioni G, Puppi G (1988). Ecologia degli endofiti vescicolo-arbuscolari in Italia Centrale. *Micologia e Vegetazione Mediterranea* 3:133-142
- Peterson RL, Ashford AE, Allaway G (1985) Vesicular-arbuscular mycorrhizal associations of vascular plants on Heron Island. A Great Barrier Coral Cay. *Aust J Bot* 33:669-676
- Puppi G (1982) L uso delle micorrize vescicolari-arbuscolari nel recupero di terreni sabbiosi, erosi, di discarica e di miniera. *Mic. Ital.* 2:5-10.
- Puppi G, Tabacchini P, Riess S, Sanvito A (1986a) Seasonal patterns in mycorrhizal association in a maritime sand dune system. In: Gianninazzi-Pearson V, Gianninazzi S (eds). *Physiological and Genetical aspects of Mycorrhizae*. Paris, INRA. pp. 245-251

- Puppi, G, Chiapperi F, Tabacchini P, Sanvito A, Carpigo F (1986b) Endogonaceae del litorale tirrenico. *Mic. Ital.* 2:7-14
- Puppi G, Riess S (1987) Role and ecology of VA mycorrhizae in Sand Dunes. *Angew Botanik* 61:115-126
- Read DJ (1989) Mycorrhizas and nutrient cycling in sand dune ecosystems. *Proc Roy Soc Edinburgh* 96B:89-110
- Rose SL (1988) Above and belowground community development in a marine sand dune ecosystem. *Plant Soil* 109:215-226
- Sigüenza C, Espejel I, Allen EB (1996) Seasonality of mycorrhizae in coastal sand dunes of Baja California. *Mycorrhiza* 6:151-157
- St John TV, Koske RE (1988) Statistical treatment of Endogonaceous spore counts. *Trans Brit Mycol Soc* 91:117-121
- Stahl E (1900) Der Sinn der Mycorrhizen bildung. eine vergleichend-biologische Studie. *Jahrbuch für Wissenschaftliche Botanik* 34:539-668
- Stürmer SL, Bellei MM (1994) Composition and seasonal variation of spore populations of arbuscular mycorrhizal fungi in dune soils on the island of Santa Catarina, Brazil. *Can J Bot* 72:359-363
- Sutton JC, Sheppard BR (1976) Aggregation of sand-dune soil by endomycorrhizal fungi. *Can J Bot* 54:326-333
- Sylvia DM (1986) Spatial and temporal distribution of vesicular-arbuscular mycorrhizal fungi associated with Uniola paniculata in Florida foredunes. *Mycologia* 78(5):728-734
- Sylvia DM (1989) Nursery inoculation of sea oats with vesicular-arbuscular mycorrhizal fungi and outplanting performance on Florida beaches. *J Coastal Res* 5:747-754

- Sylvia DM, Will ME (1988) Establishment of vesicular-arbuscular mycorrhizal fungi and other microorganisms on a beach replenishment site in Florida. *Appl Env Microbiol* 54:348-352
- Sylvia DM, Burks JN (1989) Selection of vesicular-arbuscular mycorrhizal fungi for inoculation of Uniola paniculata L. *Mycologia* 80:565-568
- Sylvia DM, Jarstfer AG, Vosástka M (1993) Comparisons of vesicular-arbuscular mycorrhizal species and inoculum formulations in a commercial nursery and on diverse Florida beaches. *Biology and Fertility of Soils* 16:139-144
- Tews LL, Koske RE (1986) Toward a sampling strategy for vesicular-arbuscular mycorrhizas. *Trans Brit Mycol Soc* 87:353-358
- Webley DM, Eastwood DJ, Gimingham CH (1952) Development of a soil microflora in relation to plant succession on sand-dunes, including the rhizosphere flora associated with colonizing species. *J Ecol* 40:168-178
- Will ME, Sylvia DM (1990) Interaction of rhizosphere bacteria, fertilizer, and vesicular-arbuscular mycorrhizal fungi with sea oats. *Appl Env Microbiol* 56:2073-2079

Arbuscular Mycorrhizae in a Tropical Sand Dune Ecosystem on the Gulf of Mexico. I. Mycorrhizal status and mycorrhizal inoculum potential along a successional gradient

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Abstract Root samples of 37 species distributed at the beach and along a successional gradient (from mobile to stabilized areas) in a tropical sand dune system on the Gulf of Mexico were collected to determine their mycorrhizal status. Since 97% of the species were recorded as mycorrhizal, our results support the high percentage of mycorrhizal species found in other dunes of the world.

The mycorrhizal inoculum potential of the sand from several dune areas was compared through two different bioassays. The first one was conducted by measuring the field rate of colonization by arbuscular mycorrhizal fungi in Chamaecrista chamaecristoides transplanted seedlings to plots previously distributed at random in the foredunes and in the mobile area. The seedlings were harvested every 8 days during three weeks to record mycorrhizal structures. In the mobile area, no mycorrhizal colonization was observed during the 21 days of the experiment. In the foredunes, hyphae and external mycelium were present in 40% of the seedlings as early as eight days after transplanting. Fifteen days after transplanting, arbuscules and vesicles were observed in 60 and 20% of the seedlings respectively. 100, 46 and 20% of the seedlings showed hyphae, arbuscules and vesicles, respectively, 21 days after transplanting.

The second bioassay was conducted by transplanting maize seedlings to pots previously filled with sand from the foredunes, mobile dunes, grassland and a Dyphisa robinoides shrub area. One month after transplanting, the lowest mycorrhizal inoculum potential was found in the mobile dunes and the highest in the shrub area. As expected, the mycorrhizal inoculum potential increased with dune stabilization.

Key words Tropical sand dunes, Arbuscular mycorrhizae, mycorrhizal inoculum potential, field colonization rate.

Introduction

In coastal sand dune ecosystems pioneer plants are subjected to considerable stress from deficiency in the major nutrients (N, P, K) and organic matter, wide fluctuation in soil moisture and temperature, injury from sand blasting and salt spray as well as excessive erosion or accretion (Chapman 1976; Moreno-Casasola 1982; Barbour et al. 1985; Maun 1994). It has been widely accepted that arbuscular mycorrhizae are important for seedling survival as well as for establishment and growth, particularly in marginal habitats, since the symbiosis improves stress tolerance (Daft et al. 1975; Rozema et al. 1986; Allen 1991; Barea and Jeffries 1995; Koske and Gemma 1995).

Previous studies on mycorrhizae in sand dune ecosystems have shown that most of the colonizing plants are heavily infected by arbuscular mycorrhizal fungi (AMF) (Koske et al. 1975; Giovannetti and Nicolson 1983; Giovannetti 1985; Peterson et al. 1985; Puppi and Riess 1987; Koske 1988; Dalpé 1989; Koske and Halvorson 1989; Logan et al. 1989; Louis 1990; Gemma and Koske 1992). Examination of root samples from the coastal dunes of Scotland indicated that the degree of AMF colonization varied with respect to the plant succession, increasing from the foredunes to the fixed dunes (Nicolson 1960). Further studies have also concluded that the infection percentage of roots and the spore abundance of AMF varies according to the position and season in these ecosystems (Nicolson and Johnston 1979; Jehne and Thompson 1981; Giovannetti and Nicolson 1983; Ernst et al. 1984; Giovannetti 1985; Puppi et al. 1986; Sylvia 1986; Gemma and Koske 1988; Koske and Halvorson 1989). However, almost all we know about mycorrhizae in sand dunes comes from temperate environments (e.g. Forster 1979; Forster and Nicolson 1981a, b; Bergen and Koske 1984; Ernst et al. 1984; Koske 1987; Koske and Tews 1987; Sylvia 1986; Gemma and Koske 1988, 1989; Gemma et al. 1989; Koske and Halvorson 1989; Blaszkowski 1994; see references in section 2.7).

In the Gulf of Mexico, there is a tropical sand dune system with a very complex topography related to a high diversity of plant species, which includes all stages of stabilization (from mobile to fixed dunes) (Moreno-Casasola et al. 1982; Moreno-Casasola and Espejel 1986). Studies on mycorrhizae in this Mexican sand dune flora had not been conducted previously. This paper reports the occurrence of arbuscular mycorrhizal fungi in several species which are distributed in different successional stages of this ecosystem and compares the mycorrhizal inoculum potential of the sand from four different areas. Since in addition to spores, infected roots and mycelia in the soil can function as mycorrhizal propagules (Read et al. 1976), inoculum potential was measured by bioassay experiments of extracted soils and intact substrates in field observations of infection rate.

Because of the low nutrient content of the sand dune substrates of this tropical ecosystem (Moreno Casasola et al. 1982; Valverde 1992), a high percentage of species are expected to be associated to AMF. We also predict higher mycorrhizal inoculum potential with dune stabilization.

Materials and methods

Study site

The study was conducted in the biological station "Centro de Investigaciones Costeras de La Mancha" (CICOLMA). It is situated in the central part of the state of Veracruz, on the Gulf of Mexico (19°36'N, 96°22'40"W) (Fig. 1). The climate belongs to Koëppen type Aw₂ (Tropical forest climate, warm with seasonal rain in summer, although about 10% of precipitation falls in the winter) and the mean annual temperature and total annual precipitation are 22 to 26 °C and 1200 to 1500 mm., respectively (Gómez-Pompa 1972; Moreno-Casasola 1982). In this area, it is possible to identify three distinctive climatic periods: The dry season (from March to May), with high temperatures (24 °C), minimum

precipitation (6 mm) and high wind velocity (6.1 m/s); the rainy season (from June to October), with high temperature (26 °C), maximum precipitation (200-400 mm) and minimum wind velocity (3.8 m/s); and the "Nortes" (windy) season (from November to February) with temperatures of 20 °C, average precipitation of 24 mm and maximum wind velocity (7m/s) (Carabias and Castillo 1982).

Because the prevailing winds come from the North (not from the ocean), the sand dunes of CICOLMA are of the parabolic type and are oriented N-S (Moreno-Casasola 1982). Moreno-Casasola and Espejel (1986) defined six zones considering sand movement, salinity and depth of the water table: The beach, embryonic dunes and foredunes, blowouts and active dunes, humid and wet slacks, sheltered zone behind the foredunes and fixed dunes. Because of the temperature and precipitation regimes, this area is surrounded by tropical semi-deciduous forest. A detailed description of the vegetation and physical factors of La Mancha is found in Moreno-Casasola (1982); Moreno-Casasola et al. (1982); Moreno-Casasola (1986); Moreno Casasola and Espejel (1986); Moreno-Casasola (1988) and Dubroeuq et al. (1992).

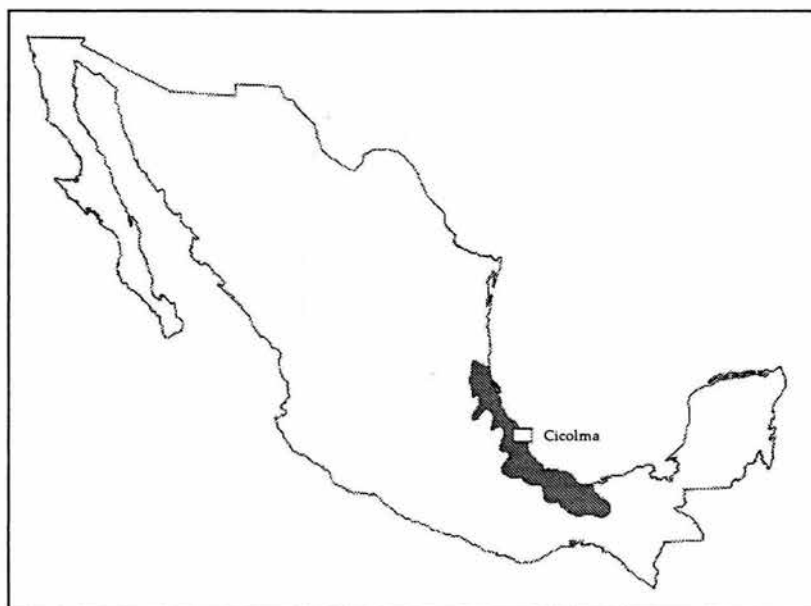


Fig. 1 Localización del sistema de dunas en el Centro de investigaciones costeras de La Mancha (CICOLMA)

Root sampling and mycorrhizal colonization

Root samples of 37 species were cut directly from plants collected at the beach, embryo dunes and foredunes, mobile and semi-mobile area, grassland, wet slacks and fixed dunes on July 1991, October 1991, April 1994 and/or August 1994 (mainly during the rainy season) (Fig.2, 3).

To analyse the successional and seasonal patterns of colonization by arbuscular mycorrhizal fungi, roots from three endemic species, which are distributed in different areas of the dunes were sampled in May and September 1994 (dry and rainy season, respectively). Attempts were made to sample in the windy season but fine fresh roots were very hard to find. The species were: Trachypogon gouinii Fourn. ex Hemsl. (Gramineae) which was collected in the foredunes, mobile and a stabilized area; Palafoxia lindenii Gray (Compositae) which could be found in the foredunes, embryo dunes and mobile areas and Chamaecrista chamaecristoides (Collad.) I. and B. (Leguminosae) which was sampled in the mobile dune.

At the moment of sampling, the roots were stored in 50% alcohol. For the AMF colonization assessment, they were taken to the laboratory where they were cleared and stained with trypan blue following the procedure suggested by Koske and Gemma (1989). The root segments were subsampled and cut into 1 cm segments and they were mounted on microscope slides in acid glycerol to be examined in a microscope fitted with Nomarski differential interference contrast optics (40-100x). AMF colonization percentage was measured using the line intersection method (Giovannetti and Mosse 1980). Mycorrhizal structures (hyphae, hyphal coils, vesicles or arbuscules) were only scored when they crossed the grid-line, and the percentage was calculated based upon the number of segments containing internal structures out of the intersections examined.

For the species survey, mycorrhizal colonization was measured in 100 root segments taken at random from a compound sample of at least three individuals per species.

To compare the colonization percentages by AMF of *T. gouinii*, *P. lindenii* and *C. chamaecristoides* in the different seasons and dune areas, 50 root segments out of 5 individuals per species and zone were reviewed.

The non-parametric analysis of variance (Kruskall-Wallis test) was used to detect significant differences in the AMF colonization percentages of *T. gouinii* among the three different areas and between the dry and rainy season. In *P. lindenii* and *C. chamaecristoides* the Mann-Whitney test was used for the same purpose (Zar 1974).

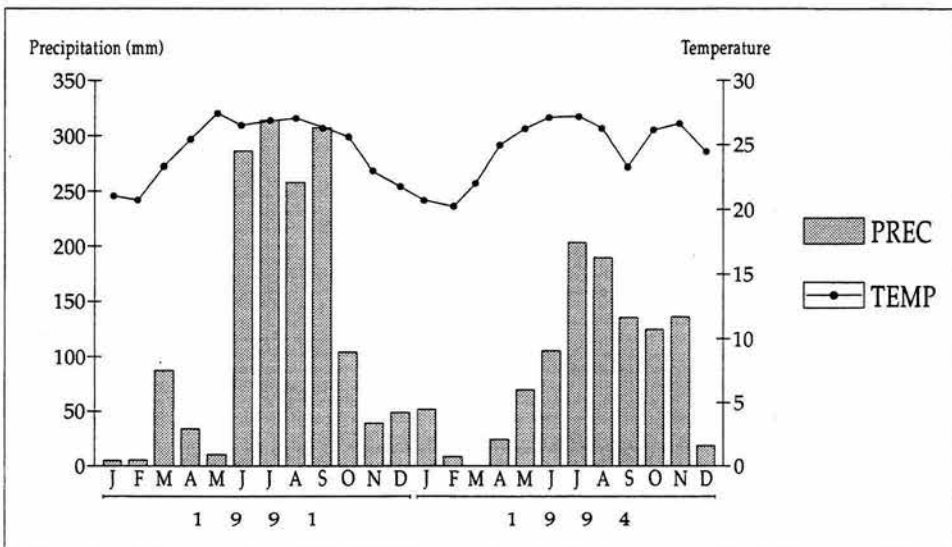


Fig. 2 Temperature and precipitation regimes of the years of root collection

Centro de investigaciones costeras de La Mancha

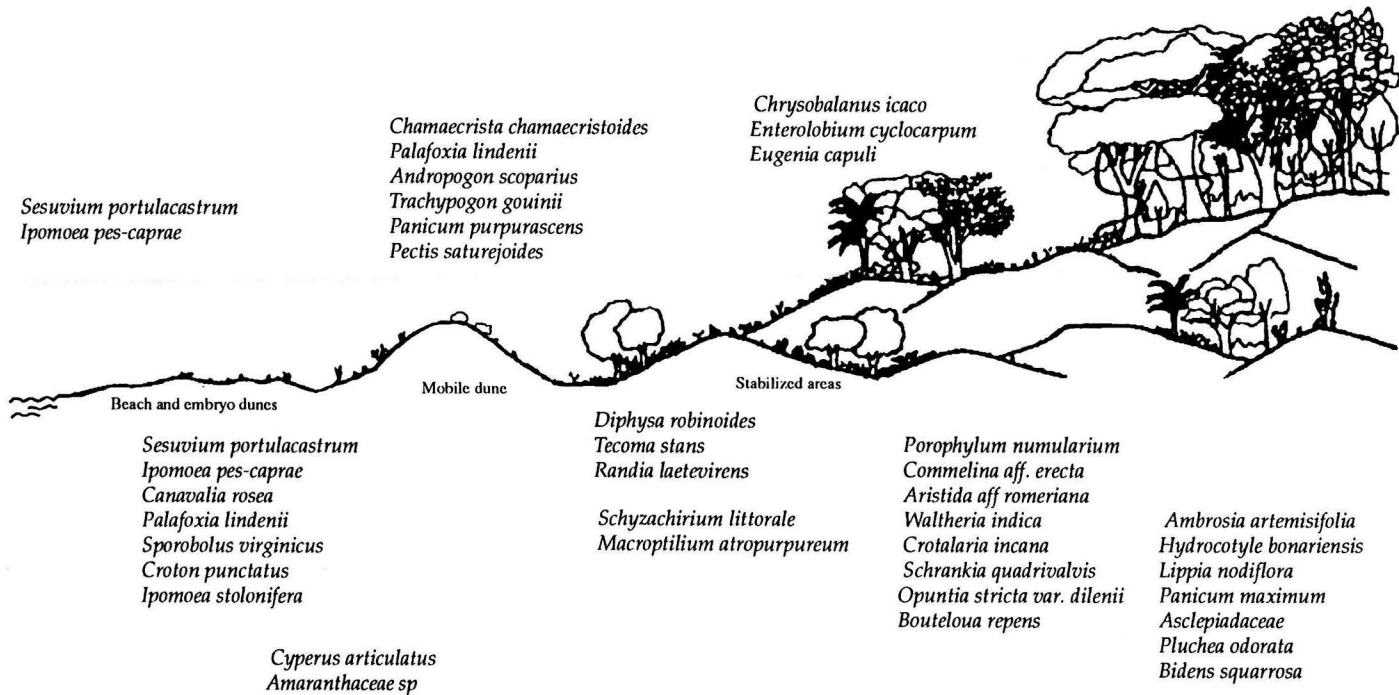


Illustration taken from Acosta (1993) with permission

Fig. 3 Sites of root collection

Mycorrhizal inoculum potential from different successional areas

To determine the mycorrhizal inoculum potential of the beach and different successional areas of the tropical dune system, two different experiments were undertaken:

Experiment 1: Pot Bioassay

Sand was collected at the end of the 1991 rainy season. It was taken directly from the rhizosphere of plants distributed in the foredunes, mobile dunes, grassland and a Dyphisa robinoides (Leguminosae) shrub area. Since the sand was not sifted, root fragments were present. The nutrient content of the sand from each area has been reported by Moreno-Casasola et al. 1982, Kellman and Roulet (1990) and Valverde (1992). Valverde (1992) found that although the organic matter content increased from the mobile to the stabilized area, the value obtained at the beach was not different from that of the stabilized area. Very low values of PO_4 have also been reported around the dune system, ranging from 0.46, 0.81 to 1.49 ppm at the beach, mobile and a stabilized area, respectively, but with no significant differences among the areas.

Twenty black plastic bags were filled with 3 l. of sand from each area and one 3 day-old maize seedling was transplanted into each. All of the pots were distributed at random outside the greenhouse of the biological station CICOLMA, so they were subjected to the natural temperature regimes of the sand dune system (Fig. 2). Three plants were randomly chosen to be harvested one week and one month after transplanting (3 plants X 4 areas X 2 harvests). Roots were separated and processed as explained above. 100 root segments per replicate were selected at random to assess AMF colonization percentage, but in addition to the frequency of infection ($F\% = \text{Numbers of segments containing AMF structures out of every 100 intersections examined}$), the density of root colonization (proportion of the root cortex occupied by AMF, $M\%$) was determined following the procedure suggested by Trouvelot et al. (1986):

$M\% = (95n_5 + 70n_4 + 30n_3 + 5n_2 + n_1)/N$; where N is the number of segments observed and n_1, n_2, \dots, n_5 are the numbers of segments recorded with 0, 1, 2, ... 5. (0: No infection; 1: trace; 2: less than 10%; 3: 11 to 50%; 4: 51 to 90%; 5: more than 90%).

The non-parametric analysis of variance (Kruskall-Wallis test) was used to determine significant differences among areas in each harvest (Zar 1974).

Experiment 2: Rate of colonization by AMF in the foredunes, mobile dune and grassland

To compare how long it takes for a seedling to become colonized by AMF in the different natural areas of the dune system, three 2 X 2 m plots were distributed at random at the beach, in an area covered by Sporobolus virginicus, Canavalia rosea and Ipomoea pes-caprae; in the mobile dune and in a Trachypogon gouinij grassland zone. Each square was divided into 20 cm grids and one five day-old seedling of Chamaecrista chamaecristoides was transplanted at the center of each square in October 1994. This date represents the end of the rainy season, which is one of the natural periods of germination and establishment for that species (Martínez and Moreno-Casasola 1993). To ensure seedling survival, the plants were artificially watered every second day and shading was avoided by previously removing the aerial part of the vegetation of the foredunes and grassland zone. Since this was done without disturbing the ground, the natural inoculum potential of hyphal network and/or spores was preserved in each square. In the sites distributed in the mobile dune, plant removal was not needed because it was an area without vegetation.

Five seedlings for each quadrat (15 per area) were randomly chosen to be harvested at intervals of 7 days, for three weeks. Their roots were carefully separated and fixed and stained by the methods described above. Presence of arbuscular mycorrhizal structures was scored. Because of the small size of the roots, no attempts were made to record colonization percentage. Results from the grassland zone are not reported because enough seedling replicates did not survive in this area, probably as a result of herbivory.

Results

Mycorrhizal Status

The mycorrhizal structures and colonization values of the species distributed along the different successional stages of the sand dunes of CICOLMA are shown in Table 1 (see plates). Ninety seven percent of the species sampled were associated with arbuscular mycorrhizal fungi, including members of reported non-mycorrhizal families such as Aizoaceae, Commelinaceae, Convolvulaceae and Cyperaceae (Gerdemann 1968, Trappe 1987).

At the beach, embryo dunes and foredunes, only Ipomoea stolonifera formed no mycorrhizae. Only hyphae were found in a low percentage of its roots. All of the species collected in the mobile dune and stabilized areas, were colonized by AMF structures.

The colonization percentages by AMF of Trachypogon gouinii, Palafoxia lindonii and Chamaecrista chamaecristoides, which were collected in different successional areas of the sand dune system in the rainy and dry season are shown in Table 2. In T. gouinii there were no statistically significant differences among the percentages of colonization registered in the foredunes, mobile and grassland areas sampled or between the two different seasons considered. Low colonization percentages were observed in P. lindonii roots which were collected in the embryo dunes in September. In contrast, the colonization percentage scored in C. chamaecristoides in May, was significantly lower from that obtained in September.

Table 1. Collection sites, collection dates, Colonization percentages by AMF and mycorrhizal structures found in plants distributed in different successional stages of a tropical sand dune ecosystem on the Gulf of Mexico. Nomenclature is in accordance to Moreno-Casasola et al. 1982

FAMILY Species	Collection site	Collection date	AMF colonization percentage	Hyphae	Hyphal coils	Vesicles	Arbusc
AIZOACEAE <i>Sesuvium portulacastrum</i>	Drift line and embryo dunes	Apr/94	19%	X	X	X	
ASCLEPIADACEAE Asclepiadaceae	Wet slack	Aug/94	41%	X		X	
BIGNONIACEAE <i>Tecoma stans</i> *	Stabilized area	Aug/94	--	X		X	
CACTACEAE <i>Opuntia stricta</i> var. <i>dillenii</i>	Stabilized area	Jul/91	33%	X		X	
COMMELINACEAE <i>Commelina aff. erecta</i>	Stabilized area	Oct/91	30%	X		X	
COMPOSITAE <i>Ambrosia artemisifolia</i>	Stabilized area	Ago/94	84%	X	X	X	
<i>Bidens pilosa</i>	Wet slack	Jul/91	36%	X	X	X	X
<i>Florestina tripteris</i>	Stabilized area	Jul/91	12%	X		X	
<i>Palafoxia lindenii</i>	Embryo dunes	Aug/94	16%	X	X	X	X
<i>Pectis saturejoides</i>	Mobile dunes	Oct/91	84%	X	X	X	X
<i>Pluchea odorata</i> *	Stabilized area	Ago/94	--	X		X	
<i>Porophyllum nummularium</i>	Stabilized area	Jul/91	42%	X		X	X
CONVOLVULACEAE <i>Ipomoea pes-caprae</i>	Embryo dunes	Jul/91	39%	X	X	X	
<i>Ipomoea stolonifera</i>	Embryo dunes	Jul/91	3%	X			
CYPERACEAE <i>Cyperus articulatus</i>	Beach	Jul/91	8%	X		X	
EUPHORBIACEAE <i>Croton punctatus</i>	Embryo dunes	Oct/91	24%	X	X		
Euphorbiaceae	Beach		31%	X			

GRAMINEAE

<i>Aristida aff. romeriana</i>	Stabilized area	Jul/91	62%	X		X	
<i>Bouteloua repens</i>	Stabilized area	Jul/91	18%	X	X	X	X
<i>Panicum purpurascens</i>	Mobile dune	Jul/91	76%	X	X	X	X
<i>Trachypogon gouinii</i>	Mobile dune	Jul/91	12%	X		X	X
<i>Schyzachirium sp.</i>	Stabilized area	Jul/91	43%	X	X	X	X
<i>Sporobolus virginicus</i>	Beach	Jul/91	48%	X	X	X	X

LEGUMINOSAE

<i>Canavalia rosea</i>	Beach, foredunes			X		X	X
<i>Chamaecrista chamaecristoides</i>	Mobile dune	Jul/91	86%	X		X	
<i>Crotalaria incana</i>	Stabilized area	Jul/91	84%	X		X	
<i>Diphysa robinoides</i>	Dyphisa shrub	Jul/91	31%	X		X	
<i>Enterolobium cyclocarpum</i>	Stabilized area	Ago/94	58%	X		X	
<i>Macroptilium atropurpureum*</i>	Stabilized area	Jul/91	--	X		X	
<i>Schrankia quadrivalvis</i>	Stabilized area	Jul/94	36%	X		X	

MYRTACEAE

<i>Eugenia capuli*</i>	Wet slack	Ago/94		X		X	
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ROSACEAE

<i>Chrysobalanus icaco*</i>	Stabilized area	Ago/94		X		X	
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RUBIACEAE

<i>Randia laetevirens*</i>	Stabilized area	Ago/94		X		X	
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STERCULIACEAE

<i>Walteria indica</i>	Stabilized area	Jul/91	28%	X	X	X	X
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TURNERACEAE							
<i>Turnera ulmifolia</i>	Stabilized area	Jul/91	32%				
UMBELLIFERAE							
<i>Hydrocotyle bonariensis</i>	Wet slack	Ago/94	76%	X	X	X	X
VERBENACEAE							
<i>Lippia nodiflora</i>	Wet slack	Ago/94	48%	X	X	X	X

Note: Species with * were collected from seedlings and not enough segments were present to assess mycorrhizal colonization.

Table 2. Range of AMF colonization percentages of *Trachypogon gouinii*, *Palafoxia lindenii* and *Chamaecrista chamaecristoides* which were sampled in different successional areas of the tropical sand dune ecosystem of La Mancha, Veracruz during the dry (May) and the rainy (September) season. Discontinuous lines indicate significant differences between seasons, according to the Mann-Whitney test ($p < 0.05$). The last column indicates significant ($p < 0.05$ (*)) or non-significant (n.s.) differences between areas, according to the non-parametric Kruskal-Wallis or Mann-Whitney test (see text).

Species	Sampling date	Foredunes	Mobile dune	Stabilized area	Level of significance
<i>Trachypogon gouinii</i>	May	(30 - 64)	(30 - 78)	(28 - 72)	n.s
	Sep	(24 - 68)	(40 - 72)	(44 - 85)	n.s
<i>Palafoxia lindenii</i>	May	(2 - 40)	(0 - 6)		n.s
	Sep	(8 - 60)	(10 - 30)		*
<i>Chamaecrista chamaecristoides</i>	May		(30 - 64)		
	Sep		(2 - 34)		

Mycorrhizal inoculum potential

Experiment 1: Pot Bioassay

The values of the colonization percentages and the density of maize root cortex colonized by AMF which were scored 8 and 30 days after seedling transplanting in sand from four different areas (foredunes, mobile dune, grassland and shrub area) are shown in Table 3. In the first harvest, 8 days after transplanting, an average of 10% root infection was found in all the areas, with a density of root colonization ranging from 0.3% in the foredunes to 2 % in the grassland. Due to the wide variation among replicates, there were no statistically significant differences in the AMF colonization percentages of the four different substrates. On the second harvest, one month after transplanting, the lowest inoculum potential was observed in the mobile area and the highest in the shrub area of *Diphysa robinoides* ($p < 0.05$). Similarly, the density of root colonization was lower in the mobile dune and higher in the shrub area ($p < 0.05$) (Table 3).

Table 3. Range of colonization percentage (F%) and density of root cortex colonized by arbuscular mycorrhizal fungi (M%) scored in maize plants which were transplanted to four kind of substrates collected in different successional areas of the tropical sand dune ecosystem of La Mancha, Veracruz, México. Different letters indicate significant differences among the areas ($p < 0.05$), according to the non-parametric analysis of variance (Kruskall-Wallis test).

	8 days F%	8 days M%	31 days F%	31 days M%
Embryo dunes	a (3 - 18)	a (0.07 - 0.8)	a (29 - 59)	a (7 - 8)
Mobile dune	a (1 - 8)	a (0.01 - 1)	b (12 - 30)	b (2 - 3)
Grassland	a (0 - 26)	a (0 - 6)	a (42 - 60)	c (4 - 5)
<i>Diphysa robinoides</i> shrub area	a (7 - 13)	a (0.4 - 1)	c (80 - 85)	d (13 - 17)

Experiment 2: Field bioassay

In the foredunes, external mycelium and internal hyphae were present since the first week in 40% (33 ± 10) of the seedlings. Nine out of fifteen seedlings (60%) had arbuscules in the second harvest (15 days after transplanting). Three weeks after transplanting, hyphae, arbuscules and vesicles were registered in 100%, 46 and 20 % of the seedlings respectively (Fig. 4). In contrast, in the mobile area, no mycorrhizal structures were recorded during the 21 days of the experiment.

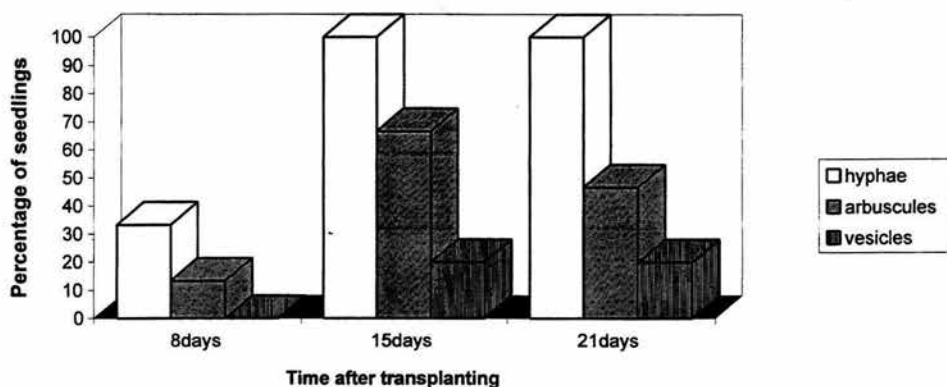


Fig. 3 Percentage of *Chamaecrista chamaecristoides* seedlings with mycorrhizal structures (Hyphae, arbuscules and vesicles) 7, 14 and 21 days after being transplanted to the foredunes.

Discussion

The high percentage of species with arbuscular mycorrhizae found in this tropical sand dune system is consistent with the high percentage of mycorrhizal species in other dunes throughout the world, either temperate or sub-tropical (Koske et al. 1975; Giovannetti and Nicolson 1983; Giovannetti 1985; Peterson et al. 1985; Puppi et al. 1986; Puppi and Riess 1987; Koske 1988; Dalpé 1989; Koske and Halvorson 1989; Logan et al. 1989; Louis 1990; Gemma and Koske 1992). Species of Cyperaceae, Convolvulaceae and Commelinaceae families, considered mainly as non-mycotrophic, have also been reported as mycorrhizal in other dune systems (Logan et al. 1989; Read 1989).

At the beach, close to the high tide mark, the tropical sand dune of La Mancha is mainly colonized by Sesuvium portulacastrum (Moreno-Casasola and Espejel 1986). This species is a succulent member of the Aizoaceae family (which is considered to include mainly nonmycorrhizal plants) (Gerdemann 1968). Although in the sand dunes of Hawaii (Koske and Gemma 1990) and Singapore (Louis 1990), this species is reported as non-mycorrhizal, AMF hyphae and vesicles were found in some of our samples. Hyphal coils and vesicles have also been reported in the individuals of S. portulacastrum collected in the coastal sand dunes of New South Wales in Australia (Logan et al. 1989) and in a salt marsh of the Ganges river in India (Sengupta and Chauduri 1990). In Veracruz, Mexico, S. portulacastrum can be found in monospecific patches, forming small hummocks in the beach or in association with Ipomoea pes-caprae (close to the sea) and with Palafoxia lindenbergii (towards the embryo dunes) (Moreno-Casasola and Espejel 1986; Moreno-Casasola 1988). AMF in non-mycorrhizal species have also been found when they are growing with infected neighbours (Read 1989). Other studies concerning the mycorrhizal status of species distributed at the drift lines have yielded contrasting results. While in European sand dunes, these sites have been reported to be colonized by members of non-mycorrhizal families (Chenopodiaceae, Cruciferae and Caryophyllaceae) (Stahl 1900; Giovannetti and Nicolson 1983; Read 1989), in Hawaii, most of the seedlings growing in the drift line area

were associated with AMF (Koske and Gemma 1990; Gemma and Koske 1992). In La Mancha, it has been noted that the same stolons of I. pes-caprae show lower AMF colonization percentages at the beach, towards the drift line, than in the embryo dunes and foredunes (Reynaldo García, personal communication).

Out of the species sampled at the beach, embryo dunes and foredunes, only I. stolonifera was non-mycorrhizal. All of the other species, Ipomoea pes-caprae, Canavalia rosea, Sporobolus virginicus, Croton punctatus and Palafoxia lindenii were colonized by AMF. Nicolson (1960) also stressed the surprisingly high levels of AMF colonization of the pioneer embryo dunes. S. virginicus has also been reported as mycorrhizal in Heron Island on Australian coast (Peterson et al. 1985) and in Hawaiian sand dunes (Koske and Gemma 1990), Canavalia rosea in Australia (Logan et al. 1989) and I. pes-caprae in Singapore (Louis 1990). Contrasting mycorrhizal status between different species of the same genus Ipomoea (I. pes-caprae, mycorrhizal; I. stolonifera, nonmycorrhizal) has also been reported in Australian sand dunes with I. brasiliensis and I. cairica (Logan et al. 1989).

The high percentage of mycorrhizal species in this area is consistent with the high mycorrhizal inoculum potential shown by the bioassay and by the infection rate field experiment at the end of the rainy season.

Considering the mobile and semi-mobile areas of this tropical dune system, it is important to stress that despite the low mycorrhizal inoculum potential shown by the bioassay in these areas, all of the species collected in the mobile dune, Chamaecrista chamaecristoides, Palafoxia lindenii, Pectis satureioides, Schizachyrium sp., Trachypogon guoinii and Panicum purpurascens were heavily colonized by AMF structures, as demonstrated by the high values of colonization of most of them. These species were mainly collected towards the arms and crests of the mobile dune. However, it is interesting to realize that the average colonization percentages of T. guoinii which were scored in the mobile area were not statistically different from those obtained at the beach and in the grassland zone in any of the two sampling dates. This contrasts with the results obtained in other dunes around the

world, where percentages of AMF colonization in plants distributed in sites with low plant density are lower than those in areas with high density of plants (Nicolson 1960; Nicolson and Johnson 1979; Koske and Halvorson 1981; Koske and Polson 1984).

The unlikeliness of association with AMF in the mobile dune, observed in the field experiment on infection rate, could be explained by the fact that the seedlings were transplanted in the most mobile and unstable part of the dune, where no vegetation was present. It seems that one of the sources of inoculum of the plants distributed in the mobile dunes could be the infected roots and the external mycelium of previously established individuals, in this case mainly the roots of C. chamaecristoides, since this species is the first colonizer of the mobile areas, and once it is established other species are able to colonize (Moreno-Casasola and Espejel 1986). We have compared the mycorrhizal infection of Panicum purpurascens seedlings collected near and far from C. chamaecristoides and have found that those which are close become infected while the others do not (see plates). Similarly, colonization by AMF in Festuca rubra was more extensive when the plant was establishing under Ammophila arenaria at British sand dunes (Read 1989). However, additional experiments are required to confirm this hypothesis in the sand dunes on CICOLMA.

As expected, the mycorrhizal inoculum potential increased in the successional gradient from the mobile to the stabilized areas of the dune system (grassland and shrub area) and all the species sampled in these sites were associated to arbuscular mycorrhizal fungi.

The seasonal pattern of root colonization by AMF, which was expected in these sand dunes, due to the marked differences between the dry and rainy seasons, could not be determined from this experiment in all the species sampled. Only C. chamaecristoides increased the values of AMF colonization in the rainy season, coinciding with its flowering period (Castillo and Carabias 1982). However, it should be kept in mind that fine fresh roots were not available in the dry-windy season. Therefore, it is likely that in this season the percentages of AMF colonization are very low, due to the drier conditions with poor

root plant growth. In addition, the presence of infection does not necessary imply physiological activity, and it would be helpful to quantify the proportion of hyphae, vesicles, arbuscules and hyphal coils, as well as their viability, in each date, to investigate the seasonal patterns of infection of this tropical dune system.

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References

- Allen M. F. (1991) *The ecology of mycorrhizae*. Cambridge University Press
- Barbour MG, De Jong TM, Pavlick BM (1985) Marine beach and dune plant communities. In: Chabot BF, Mooney HA (eds) *Physiological ecology of North American plant communities*. Chapman and Hall, New York, London, pp 297-322
- Barea JM, Jeffries P (1995) Arbuscular mycorrhizas in sustainable soil-plant systems. In: Varma A, Hock B (eds) *Mycorrhiza. Structure, Function, Molecular biology and Biotechnology*. Springer-Verlag, Berlin Heidelberg, pp 521-560
- Bergen M, Koske RE (1984) Vesicular-arbuscular mycorrhizal fungi from sand dunes of Cape Cod, Massachusetts. *Trans Brit Mycol Soc* 83: 157-158
- Blaszowski J (1994) Arbuscular fungi and mycorrhizae (Glomales) of the Hel Peninsula, Poland. *Mycorrhiza* 5:71-88
- Carabias J, Castillo S (1982) Ecología de la vegetación de dunas costeras: Fenología. *Biotica* 7:551-568
- Chapman VJ (1976) *Coastal Vegetation*. Pergamon Press, Oxford
- Corkidi L (1996) *Ecofisiología de asociaciones micorrícicas arbusculares en especies pioneras de un ecosistemas de dunas costeras del Golfo de México*. Ph. D. Thesis, UNAM, Mexico
- Daft MJ, Hacskeylo E, Nicolson TH (1975) Arbuscular mycorrhizas in plants colonizing coal spoils in Scotland and Pennsylvania. In: Sanders FE, Mosse B, Tinker PB (eds) *Endomycorrhizas*, Academic Press, New York and London, pp 561-580
- Dalpé Y (1989) Inventaire et répartition de la flore endomycorrhizienne de dunes et de rivages maritimes du Québec, du Nouveau-Brunswick et de la Nouvelle-Ecosse. *Nat Can* 116:219-236
- Dubroeuq D, Geissert D, Moreno P, Millot G (1992) Soil evolution and plant communities in coastal dunes near Veracruz, Mexico. *Cah. Orstom, sér. Pédol.*, vol. XXVII:237-250

- Ernst WHO, Van Duin WE, Oolbekking GT (1984) Vesicular-arbuscular mycorrhiza in dune vegetation. *Acta Bot Neerl* 33:151-160
- Forster SM (1979) Microbial aggregation of sand in an embryo dune system. *Soil Biol Biochem* 11:537-543
- Forster SM, Nicolson TH (1981a) Microbial aggregation of sand in a maritime dune succession. *Soil Biol Biochem* 13:205-208
- Forster SM, Nicolson TH (1981b) Aggregation of sand from a maritime embryo sand dune by microorganisms and higher plants. *Soil Biol Biochem* 13:199-203
- Gemma JN, Koske RE (1988) Seasonal variation in spore abundance and dormancy of *Gigaspora gigantea* and in mycorrhizal inoculum potential of a dune soil. *Mycologia* 80:211-216
- Gemma JN, Koske RE (1989) Field inoculation of American beachgrass (*Ammophila breviligulata*) with V-A mycorrhizal fungi. *J Environ Manag* 29:173-182
- Gemma JN, Koske RE (1992) Are mycorrhizal fungi present in the early stages of primary succession. In: Read DJ, Lewis DH, Fitter AH, Alexander IJ (eds) *Mycorrhizas in ecosystems*, CAB international, University Press, Cambridge, pp 183-189
- Gemma JN, Koske RE, Carreiro M (1989) Seasonal dynamics of selected species of V-A mycorrhizal fungi in a sand dune. *Mycol Res* 92:317-321
- Gerdemann JW (1968) Vesicular arbuscular mycorrhizae and plant growth. *Annu Rev Phytopathol* 16:397-418
- Giovannetti M (1985) Seasonal variations of vesicular-arbuscular mycorrhizas and Endogonaceous spores in a maritime sand dune. *Trans Br Mycol Soc* 84:679-684
- Giovannetti M, Mosse B (1980) An evaluation of techniques for measuring vesicular-arbuscular mycorrhizal infection in roots. *New Phytol* 84:489-500
- Giovannetti M, Nicolson TH (1983) Vesicular-arbuscular mycorrhizas in Italian sand dunes. *Trans Br Mycol Soc* 80:552-557

- Gómez-Pompa (1972) Estudio preliminar de la vegetación y la flora en la región de Laguna Verde, Veracruz. Informe final del convenio celebrado entre el Instituto de Biología de la UNAM y el departamento de Zoología de la Escuela Nacional de Ciencias Biológicas del IPN, dentro del proyecto Estudio Ecológico de Laguna Verde, Ver., de la Comisión Federal de Electricidad
- Jehne W, Thompson CH (1981) Endomycorrhizae in plant colonization on coastal sand dunes at Cooloola, Queensland. *Aust J Ecol* 6:221-230
- Kellman M, Roulet N (1990) Nutrient flux and retention in a tropical sand dune succession. *J Ecol* 78: 664-676
- Koske RE (1987) Distribution of VA mycorrhizal fungi along a latitudinal temperature gradient. *Mycologia* 79:55-68
- Koske RE (1988) Vesicular-Arbuscular mycorrhizae of some Hawaiian dune plants. *Pacific Sci* 42:217-229
- Koske RE, Sutton JC, Sheppard BR (1975) Ecology of Endogone in Lake Huron sand dunes. *Can J Bot* 53:87-93
- Koske RE, Halvorson WL (1981) Ecological studies of vesicular-arbuscular mycorrhizae in a barrier sand dune. *Can J Bot* 59:1413-1422
- Koske RE, Polson WR (1984) Are VA mycorrhizae required for sand dune stabilization? *Bioscience* 34:420-424
- Koske RE, Tews LL (1987) Vesicular-arbuscular mycorrhizal fungi of Wisconsin sandy soils. *Mycologia* 79:901-905
- Koske RE, Gemma JN (1989) A modified procedure for staining roots to detect VA mycorrhizas. *Mycol Res* 92:486-488
- Koske RE, Halvorson WL (1989) Mycorrhizal associations of selected plant species from San Miguel Island, Channel Islands National Park, California. *Pacific Sci* 43:32-40
- Koske RE, Gemma JN (1990) VA mycorrhizae in strand vegetation of Hawaii: Evidence for long distance codispersal of plants and fungi. *Amer J Bot* 77:466-474

- Koske RE, Gemma JN (1995) Vesicular-arbuscular mycorrhizal inoculation of Hawaiian plants: A conservation technique for endangered tropical species. *Pacific Sci* 49:181-191
- Logan VS, Clarke PJ, Allaway WG (1989) Mycorrhizas and root attributes of plants of coastal sand-dunes of New South Wales. *Aust J Plant Physiol* 16:141-146
- Louis I (1990) A mycorrhizal survey of plant species colonizing coastal reclaimed land in Singapore. *Mycologia* 82:772-778
- Martínez ML, Moreno-Casasola P (1993) Survival of seedling cohorts of a tropical legume on a sand dune system along the Gulf of Mexico: Influence of germination date. *Can J Bot* 71:1427-1433
- Maui MA (1994) Adaptations enhancing survival and establishment of seedlings on coastal dune systems. *Vegetatio* 111: 50-70
- Moreno-Casasola P (1982) Ecología de la vegetación de dunas costeras. *Factores Físicos. Biotica*: 7:577-602
- Moreno-Casasola P (1986) Sand movement as a factor in the distribution of plant communities in a coastal dune system. *Vegetatio* 65:67-76
- Moreno-Casasola P (1988) Patterns of plant species distribution on coastal dunes along the Gulf of Mexico. *J Biogeog* 15:787-806
- Moreno-Casasola P, Van der Maarel E, Castillo S, Huesca ML, Pisanty I (1982) Ecología de la vegetación de dunas costeras. Estructura y composición en el Morro de la Mancha I. *Biotica* 7:491-526
- Moreno-Casasola P, Espejel I (1986) Classification and ordination of coastal sand dune vegetation along the Gulf and Caribbean Sea of Mexico. *Vegetatio* 66:147-182
- Nicolson TH (1960) Mycorrhizae in the Gramineae, II. Development in different habitats particularly sand dunes. *Trans Br Mycol Soc* 43:132-145

- Nicolson TH, Johnston C (1979) Mycorrhiza in the Gramineae III. Glomus fasciculatus as the endophyte of pioneer grasses in a maritime sand dune. *Trans Br Mycol Soc* 72:262-268
- Peterson RL, Ashford AE, Allaway G (1985) Vesicular-arbuscular mycorrhizal associations of vascular plants on Heron Island. A greater barrier coral cay. *Aust J Bot* 33:669-676
- Puppi G, Tabacchini P, Riess S, Sanvito A (1986) Seasonal patterns in mycorrhizal association in a maritime sand dune system. In: Gianninazzi-Pearson V, Gianninazzi S (eds) *Physiological and genetical aspects of mycorrhizae*, INRA, Paris, pp 245-251
- Puppi G, Riess S (1987) Role and ecology of VA mycorrhizae in sand dunes. *Angew Botanik* 61:115-126
- Read DJ (1989) Mycorrhizas and nutrient cycling in sand dune ecosystems. *Proc Roy Soc Edinburgh* 96B:89-100
- Read DJ, Koucheiki HK, Hodgson J (1976) Vesicular-arbuscular mycorrhizae in natural vegetation systems. I. The occurrence of infection. *New Phytol* 77:641-653
- Rozema J, Arp W, Van Diggelen J, Van Esbroek M, Broekman R, Punte H (1986) Occurrence and ecological significance of vesicular arbuscular mycorrhiza in the salt marsh environment. *Acta Bot Neerl* 35:457-467
- Sengupta A, Chauduri S (1990) Vesicular arbuscular mycorrhiza (VAM) in pioneer salt marsh plants of the Ganges river delta in West Bengal (India). *Plant Soil* 122:111-113
- Stahl E (1900) Der Sinn der Mycorrhizenbildung. Eine vergleichend-biologische Studie. *Jahrbuch für Wissenschaftliche Botanik* 34:539-668
- Sylvia DM (1986) Spatial and temporal distribution of vesicular-arbuscular mycorrhizal fungi associated with Uniola paniculata in Florida foredunes. *Mycologia* 78:728-734

- Trappe JM (1987) Phylogenetic and ecological aspects of mycotrophy in the Angiosperms from an evolutionary standpoint. In: Safir GR (ed) Ecophysiology of VA mycorrhizal plants, CRC Press, Boca Raton FL, pp 5-25
- Trouvelot A, Kough J, Gianinazzi-Pearson V (1986) Mésure du taux de mycorhization VA d'un système racinaire. Recherche de méthodes d'estimation ayant une signification fonctionnelle. In: Gianinazzi-Pearson V, Gianinazzi S (eds) Physiological and genetical aspects of mycorrhizae. IESM, INRA, Paris, pp 212-222
- Valverde T (1992) Historia de vida de Schizachyrium scoparium var. littoralis en diferentes microambientes de dunas costeras. M. Sc. Thesis, UNAM, México
- Zar JH (1974) Biostatistical analysis. Prentice Hall, London

Arbuscular mycorrhizae in a Tropical Sand Dune Ecosystem on the Gulf of Mexico. II. Effects of arbuscular mycorrhizal fungi on the growth of species distributed in different successional stages

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Abstract The effects of arbuscular mycorrhizal fungi were investigated on the growth of species which are established during the first stages of colonization in different areas of a tropical sand dune system on the Gulf of Mexico. The experiment was conducted in the greenhouse of the biological station of the Centro de Investigaciones Costeras de La Mancha, comparing several parameters of plant growth in 21 and 63 day old mycorrhizal and nonmycorrhizal plants.

The leaf area and the dry biomass of root, stem and leaves of the mycorrhizal and nonmycorrhizal plants were used to calculate and compare their total dry biomass, relative growth rate, net assimilation rate, biomass allocation patterns (root/shoot, root, stem and leaf weight ratios) and mycorrhizal responsiveness. Other parameters such as leaf number and stem length were also recorded. Twenty one days after transplanting, there were no significant differences between mycorrhizal and nonmycorrhizal plants in the root, stem and leaf dry biomass in the species considered. However, forty days later, a range of mycorrhizal responsiveness was evident even in the different pioneer species. Ipomoea pes-caprae, Sporobolus virginicus and Canavalia rosea, all stoloniferous pioneer species of the beach, embryo dunes and foredunes, were less responsive to the mycorrhizal treatment, following the trend predicted for early seral species. However, the high increases of total dry biomass, and increases in the parameters related to leaf area and relative growth rate of Chamaecrista chamaecristoides, Palafoxia lindenii and Trachypogon gouinii (plants that could be found in the beach, embryo dunes and foredunes as well as in mobile dunes) suggest that mycorrhizal infection could also be crucial for the growth of early successional species.

Using the dry biomass production of the 63 day old plants, the mycorrhizal dependency of the different species, ranged from *I. pes-caprae* (-10%), *S. virginicus* (-6%), *C. rosea* (27%), *P. lindenii* (64%), *Panicum purpurascens* (64%), *C. chamaecristoides* (77%) to *T. gouinii* (84%), under the conditions tested.

Most of the species allocated the same fraction or more of dry biomass to the shoot as to the root. With the exception of *T. gouinii*, the general pattern of biomass allocation ($R/S < 1$) was not altered by the mycorrhizal treatment. However, in *C. rosea*, *S. virginicus* and *P. lindenii*, a trend to increase the allocation to the roots in the nonmycorrhizal plants was shown by the increased root weight ratios. The possible relationship between mycorrhizae and succession in this tropical sand dune ecosystem is discussed.

Key words Growth analysis, mycorrhizal responsiveness, sand dune pioneer species, succession.

"From the standpoint of plant succession on sand dunes, the fact that the development of a soil microflora is so closely associated with the vegetational succession is of considerable significance. There can be little doubt that the activity of the soil microorganisms contributes to the maturation of the habitat, and therefore constitutes a biotic factor adding its influence to the other more familiar factors causing changes in the plant communities" (Webley et al. 1952).

Introduction

Research on the role of mycorrhizae in succession in different ecosystems has provided contrasting results. The classical view proposes that early successional habitats are colonized by nonmycotrophic or facultatively mycotrophic species (Stahl 1900; Dominik 1951; Janos 1980) and has been supported by many studies (Nicolson 1960; Reeves et al. 1979; Miller 1979, 1987). However, while other investigations assure that disturbed habitats could be colonized either by mycorrhizal or nonmycorrhizal species (Pendleton and Smith 1983; Allen et al. 1984; Schmidt and Scow 1986; Allen 1987, 1988), some of the studies conducted in sand dune ecosystems suggest that arbuscular mycorrhizal association could be essential for plants that establish themselves even in the earliest seral stages of succession (Gemma and Koske 1992). Nevertheless, all the models seem to agree that in late seral stages the plants are necessarily mycorrhizal (Janos 1980; Allen and Allen 1990; Gemma and Koske 1992).

Coastal sand dunes are an ideal system for investigating the roles of mycorrhizae in succession. In these ecosystems it is possible to examine the vegetation through all the seral stages, from the pioneer to the stabilized zones, in a relatively small area. Most of the research on mycorrhizae on sand dunes includes detailed studies on the mycorrhizal status of the colonizing plants and on the identification, distribution and abundance of the spores of the arbuscular mycorrhizal fungi (AMF) which colonize the roots of those species (e.g. Nicolson 1960; Koske and Halvorson 1981; Giovannetti and Nicolson 1983; Giovannetti 1985; Gemma and Koske 1988; Dalpé 1989; Koske and Halvorson 1989; Blaszkowski

1994; Abe et al. 1994; Stürmer and Bellei 1994; Abe and Katsuya 1995). Other investigations have demonstrated that the external mycelium of the AMF plays a significant role in the process of dune stabilization, as sand grains are bound together mechanically by their hyphae into aggregates (Koske et al. 1975; Sutton and Sheppard 1976; Clough and Sutton 1978; Forster 1979; Forster and Nicolson 1981a, b). Although it has been suggested that mycorrhizae should be of great ecological significance in the nutrient uptake of plants distributed in sand dunes (Koske et al. 1975; Koske and Polson 1984; Read 1989) where the scarcity of phosphorus, nitrogen and potassium can be extreme (Willis and Yem 1961; Moreno-Casasola 1982; Kellman and Roulet 1990; Maun 1994), this has not been experimentally verified and few studies have reported their influence in the growth of sand dune species (Nicolson and Johnston 1979; Gemma and Koske 1989; Koske and Gemma 1995).

In the Gulf of Mexico, in La Mancha, Veracruz, there is a tropical sand dune system where the very complex topography creates a patchy distribution of a high diversity of plant species (Moreno-Casasola 1982; Moreno-Casasola 1986; Martínez et al. 1993). While some of them have a very restricted distribution, even in different microenvironments of the first stages of colonization, others may persist up to the stabilized areas of late stages of succession (Moreno-Casasola et al. 1982; Moreno-Casasola and Espejel 1986; Moreno-Casasola 1988). Furthermore, in contrast to temperate sand dunes, where the main stabilizing plants are members of the Gramineae (Read 1989), in the tropical sand dunes of La Mancha, different growth forms of species of Leguminosae as well as members of the Compositae, Gramineae and Convolvulaceae can be found (Moreno-Casasola and Espejel 1986; Moreno-Casasola 1988), and they were all observed as mycorrhizal in a previous study (section 3).

To test the hypothesis that plant growth response to AMF colonization increases along the successional transition from species of pioneer habitats to species of stabilized areas, the main objective of this study was to analyse the effects of mycorrhizal association on the growth of plants which are pioneers of the beach and the mobile dunes and some which can also colonize the semi-stabilized areas of this tropical sand dune ecosystem.

Materials and methods

Selected species

The species used for the growth experiment were mostly perennial plants which are established during the first stages of colonization of different areas of a tropical sand dune system on the Gulf of Mexico. They were three stoloniferous species which grow in the beach, embryo dunes and foredunes, Canavalia rosea, Ipomoea pes-caprae and Sporobolus virginicus; two endemic species of this sand dune ecosystem, Palafoxia lindenii, a low shrub which is found in the embryo dunes and foredunes, as well as in the mobile areas and Trachypogon gouinii, a rhizomatous Gramineae distributed in the foredunes, mobile dunes and in semi-stabilized areas; Chamaecrista chamaecristoides, a sand dune endemic low shrub mainly distributed in the mobile areas, and Panicum purpurascens, a clumped grass which is the only annual species included and which occurs in the mobile areas but also in more stabilized areas. The family and average seed biomass of these species is reported in Table 1.

Table 1 Species, Family and average seed biomass (g) (n = 50) of plants distributed in a tropical sand dune system on the Gulf of Mexico (Nomenclature according to Moreno-Casasola et al. 1982)

Species	Family	Average seed biomass
<i>Canavalia rosea</i>	Leguminosae	0.65
<i>Ipomoea pes-caprae</i>	Convolvulaceae	0.15
<i>Chamaecrista chamaecristoides</i>	Leguminosae	0.016
<i>Trachypogon gouinii.</i>	Gramineae	0.0017
<i>Palafoxia lindenii</i>	Compositae	0.0019
<i>Panicum purpurascens</i>	Gramineae	0.00064
<i>Sporobolus virginicus</i>	Gramineae	0.000193

Experimental procedure

The growth experiment was conducted in the greenhouse of the biological station of the "Centro de Investigaciones Costeras de la Mancha" (CICOLMA), which is situated in the state of Veracruz, on the Gulf of Mexico (19°36' N, 96°22'40"W). Detailed information about the vegetation and physical factors of the sand dunes of La Mancha can be found in Moreno-Casasola 1982; Moreno-Casasola et al. 1982; Moreno-Casasola and Espejel 1986; Moreno-Casasola 1988 and Dubroeuq et al. 1992.

Seeds of all the species were collected from at least 10 different individuals at the time of fruit ripening and 50 seeds of each were chosen at random to record their average biomass (Table 1).

The sand used for the growth experiment was collected from the foredunes and was sterilized in a dry-oven at 100 °C for 48 h. Black plastic bags were filled with 3 l of this sand and let stand for four weeks to avoid the phytotoxic effects of heating (Rovira and Bowen 1966). Chemical analysis after sterilization resulted in 16.2 ppm total phosphorus; 78.1 ppm total nitrogen and 92.5 ppm potassium; pH = 7.9 and 0.49% organic matter content (Salas 1994). No nutrient solution was added for the experiment.

Seeds were germinated at the temperature and photoperiod regimes required for each species (Martínez et al. 1992). Canavalia rosea, Ipomoea pes-caprae and Chamaecrista chamaecristoides were mechanically scarified prior to planting to obtain similar emergence times. Five days after germination ten seedlings per species were harvested and leaf area, root, stem and leaf dry weight were recorded (Initial harvest). Another 40 seedlings per species were transplanted to the black plastic bags (one per bag). At the time of transplanting, half of the bags were inoculated with an homogeneous mixture of sand collected from the rhizosphere and root fragments of plants of Palafoxia lindenii which

were distributed in the embryo dunes and foredunes (Mycorrhizal treatment, +M). The other half was not inoculated (Nonmycorrhizal treatment, -M). Spore washings were added to both treatments following the methodology of Koide and Li (1989) to reincorporate nonmycorrhizal soil microorganisms. The AMF spore species are currently being identified.

The plants were placed at random in the greenhouse of CICOLMA and they were watered every second day.

Three weeks after transplanting, some individuals of each species were harvested at random and their roots were stained with trypan blue by the procedure of Koske and Gemma (1989) to verify presence of infection.

Twenty one days after transplanting, seven replicates of mycorrhizal and nonmycorrhizal plants of some of the species (*C. chamaecristoides*, *C. rosea*, *P. lindeni* and *P. purpurascens*) were harvested to detect the effects of AMF as soon as the mycorrhizal association was verified by the presence of vesicles or arbuscules. Leaf area and the number of leaves were recorded. Roots, stems and leaves were oven dried at 80°C for 48 h. to quantify their dry biomass. Sixty-three days after germination, all the species included in the experiment were harvested as explained above (Final harvest). In *C. rosea*, *I. pes-caprae*, *C. chamaecristoides*, and *P. lindeni* the stem length was also measured.

For most of the species, seven plants per treatment of each species were used (6 species X 7 replicates X 2 treatments). However, since many of the nonmycorrhizal plants of *P. purpurascens* were severely parasitized, only four non-parasitized replicates of this species were included (1 species X 4 replicates X 2 treatments).

The data were analysed using the classical growth analysis (Hunt 1982). The initial and the final harvest were used to calculate the specific leaf area (SLA, amount of leaf area per unit leaf weight); Leaf area ratio (LAR, fraction of leaf area in the total dry weight); root weight ratio (RWR), stem weight ratio (SWR) and leaf weight ratio (LWR), the fraction of

root, stem or leaf dry biomass of the total dry biomass; relative growth rate (RGR, dry biomass gained per unit total plant dry biomass per time) and net assimilation rate (NAR, the rate of dry biomass production per unit of leaf area), (Evans 1972; Causton and Venus 1981; Hunt 1982). The NAR is only reported in the species in which the measurement of the initial leaf area was possible. In the members of the Gramineae family, the dry biomass of leaves and stems were quantified together and reported as shoot. Therefore, the specific leaf area and the leaf weight ratio were not calculated in these species.

The mycorrhizal dependency was obtained in the 63 day-old plants, from the total dry biomass as the ratio of dry mass of a mycorrhizal plant to a nonmycorrhizal plant expressed as a percentage (RFMD = Dry mass mycorrhizae plant - Dry mass nonmycorrhizal plant / Dry mass mycorrhizal plant) (Plenchette et al. 1983).

From the data obtained 21 days after transplanting, only the total dry biomass was reported. Differences between mycorrhizal and nonmycorrhizal treatments were compared using the student's *t*-test (Zar 1974).

Results

The effects of arbuscular mycorrhizal fungi on the growth and biomass allocation of species distributed on different areas of the sand dunes on the Gulf of Mexico are shown in Table 2. There were no significant differences between mycorrhizal and nonmycorrhizal treatments in the root, stem and leaf dry biomass in any of the species of the twenty one day old seedlings (data not shown) (Fig. 1). However, striking differences emerged at sixty three days, when most of the inoculated species increased their total dry biomass in different relative amounts (Table 2). Mycorrhizal plants of Chamaecrista chamaecristoides, Palafoxia lindenii, Trachypogon gouinii and Panicum purpurascens had significantly higher dry biomass of root, stem and leaves than the nonmycorrhizal plants. In T. gouinii mycorrhizal

fungi increased the biomass production more than six times, in *P. lindenii* the difference was three-fold and in *C. chamaecristoides* it was four-fold. The root dry biomass of mycorrhizal and nonmycorrhizal *Canavalia rosea* plants did not differ significantly, there was a slight increment in the leaf dry weight and the total dry biomass increased by 50%. However mycorrhizal plants of this species produced considerably longer stems (a range from 23 up to 90 cm more than the longest nonmycorrhizal stem) with considerably higher dry biomass (an average difference of 0.304 g) than the nonmycorrhizal ones (Table 2).

No improvement in the dry biomass produced with mycorrhizae was evident in *Ipomoea pes-caprae* and *Sporobolus virginicus*. In contrast to these species, all the species that increased their dry biomass production when inoculated with arbuscular mycorrhizal fungi also reached significantly higher relative growth rates in the +M treatment, ranging from *C. rosea*, (which increased its RGR by 0.005 $\text{gg}^{-1}\text{day}^{-1}$), *P. purpurascens* (0.012 $\text{gg}^{-1}\text{day}^{-1}$), *T. gouinii* (0.015 $\text{gg}^{-1}\text{day}^{-1}$), *P. lindenii* (0.019 $\text{gg}^{-1}\text{day}^{-1}$) to *C. chamaecristoides* (0.026 $\text{gg}^{-1}\text{day}^{-1}$) (Table 2).

Mycorrhizal responsiveness of the different species (which were calculated considering the total dry biomass of the 63 day-old plants) ranged from *I. pes-caprae* < *S. virginicus* < *C. roseae* < *P. lindenii* = *P. purpurascens* < *C. chamaecristoides* < *T. gouinii* (Fig. 2).

In terms of biomass allocation, in *C. Chamaecristoides* and *I. pes-caprae* both root and shoot contributed more or less equally to the final dry biomass, and there were no significant differences between treatments. However, although not significantly expressed in the root/shoot ratio values, *I. pes-caprae* reduced its allocation to the stem dry biomass when it was inoculated with mycorrhizal fungi, as demonstrated by the statistically significant differences in the averages of the stem weight ratio (SWR) (Table 2).

As shown by the root/shoot values of less than 1, *P. lindenii*, *C. rosea* and *S. virginicus* allocated more biomass to the shoots than to the roots in both treatments. *S. virginicus* (a

non responsive species) and *C. rosea* (one of the less responsive species) increased their allocation to roots when nonmycorrhizal, as demonstrated by the significant differences in the RWR values in both species and the decrease in the SWR of *S. virginicus* which also increased its root/shoot ratio (Table 2). The mycorrhizal plants of *P. purpurascens* invested more biomass to the shoot. *T. gouinii* was the only species which allocated more biomass to roots than to shoots when it was mycorrhizal. However, when nonmycorrhizal, the allocation pattern changed and the ratio became 1:1.

Inoculation with arbuscular mycorrhizal fungi significantly increased the leaf areas and the number of leaves of *C. rosea*, *C. chamaecristoides*, *P. lindenii*, *T. gouinii* and *P. purpurascens* and the leaf area of *S. virginicus*. The values of leaf area ratio also increased significantly in all the species except *I. pes-caprae* and *S. virginicus*, and the specific leaf area increased in *C. rosea*, *C. chamaecristoides* and in *P. lindenii*. The net assimilation rate did not differ between mycorrhizal and nonmycorrhizal plants in any of the species included in the experiment (Table 3).

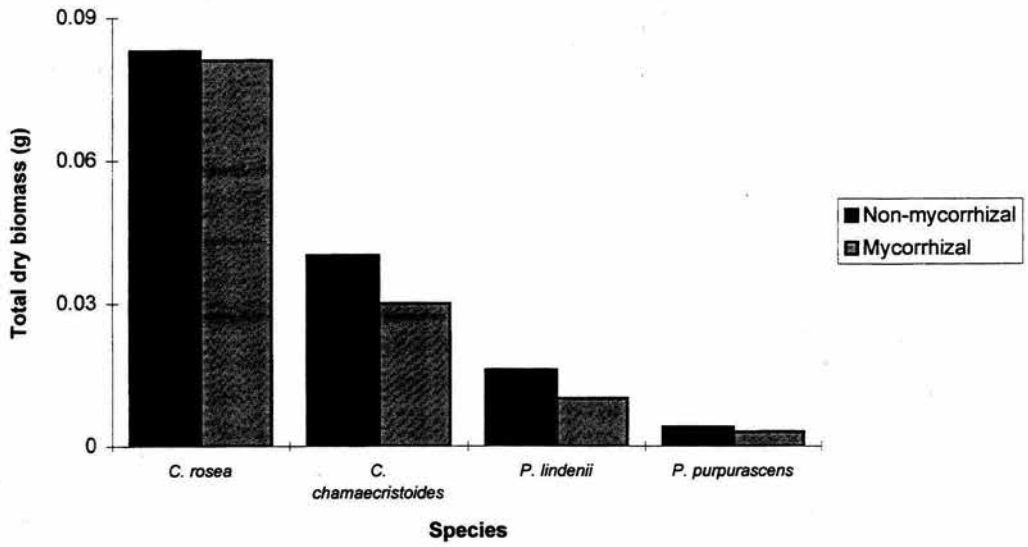
Table 2 Root (R), Stem (S) and Leaf (L) or Shoot (SH) dry biomass (g), Stem length (SL) (cm), Root weight ratio (RWR), Stem weight ratio (SWR) or Shoot weight ratio (SHWR), Leaf weight ratio (LWR) and Relative growth rate (RGR) ($\text{g g}^{-1} \text{day}^{-1}$) of mycorrhizal (+M) and non-mycorrhizal (-M) plants of different species distributed in a tropical sand dune ecosystem on the Gulf of Mexico. The data represent the average \pm standard error of seven replicates of plants which were grown for 63 days. Different letters between treatments indicate statistically significant differences according to the student's *t*-test ($p < 0.05$).

Species	Treatment	R	S	L	SL	R/S	RWR	SWR	LWR	RG
<i>Canavalia rosea</i>	+M	0.934 ^a \pm 0.16	0.768 ^a \pm 0.17	1.32 ^a \pm 0.188	65.5 ^a \pm 20.03	0.45 ^a \pm 0.06	0.31 ^a \pm 0.03	0.25 ^a \pm 0.03	0.44 ^a \pm 0.04	0.035 ^a \pm
	-M	0.774 ^a \pm 0.15	0.464 ^b \pm 0.05	0.94 ^b \pm 0.164	18.3 ^a \pm 1.89	0.54 ^a \pm 0.05	0.35 ^b \pm 0.02	0.21 ^a \pm 0.03	0.43 ^a \pm 0.04	0.030 ^b \pm
<i>Ipomoea pes-caprae</i>	+M	0.946 ^a \pm 0.34	0.402 ^a \pm 0.09	0.39 ^a \pm 0.102	10.8 ^a \pm 1.2	1.20 ^a \pm 0.21	0.53 ^a \pm 0.05	0.23 ^a \pm 0.04	0.22 ^a \pm 0.02	0.021 ^a \pm
	-M	0.855 ^a \pm 0.07	0.558 ^a \pm 0.10	0.36 ^a \pm 0.062	15.0 ^a \pm 1.4	0.95 ^a \pm 0.09	0.48 ^a \pm 0.03	0.31 ^b \pm 0.03	0.20 ^a \pm 0.02	0.022 ^a \pm
<i>Chamaecrista. chamaecristoides</i>	+M	0.180 ^a \pm 0.062	0.086 ^a \pm 0.020	0.119 ^a \pm 0.030	25.5 ^a \pm 2.92	0.93 ^a \pm 0.3	0.46 ^a \pm 0.10	0.22 ^a \pm 0.04	0.31 ^a \pm 0.08	0.083 ^a \pm
	-M	0.038 ^b \pm 0.011	0.022 ^b \pm 0.003	0.026 ^b \pm 0.006	15.0 ^b \pm 1.29	0.78 ^a \pm 0.2	0.43 ^a \pm 0.06	0.26 ^a \pm 0.07	0.30 ^a \pm 0.03	0.057 ^b \pm
<i>Palafoxia lindenii</i>	+M	0.037 ^a \pm 0.009	0.045 ^a \pm 0.006	0.046 ^a \pm 0.006	16.1 ^a \pm 1.1	0.41 ^a \pm 0.17	0.28 ^a \pm 0.08	0.35 ^a \pm 0.05	0.36 ^a \pm 0.07	0.075 ^a \pm
	-M	0.018 ^b \pm 0.006	0.012 ^a \pm 0.004	0.015 ^b \pm 0.004	10 ^b \pm 1.83	0.7 ^a \pm 0.35	0.39 ^a \pm 0.12	0.27 ^b \pm 0.05	0.33 ^a \pm 0.09	0.056 ^b \pm

Species	Treatment	R	SH	R/S	RWR	SHWR	RGR
<i>Sporobolus virginicus</i>	+M	0.049 ^a \pm 0.02	0.135 ^a \pm 0.029	0.35 ^a \pm 0.06	0.259 ^a \pm 0.034	0.740 ^a \pm 0.034	0.074 ^a \pm 0.003
	-M	0.053 ^a \pm 0.02	0.097 ^a \pm 0.029	0.55 ^b \pm 0.2	0.348 ^a \pm 0.066	0.651 ^b \pm 0.066	0.071 ^a \pm 0.003
<i>Trachypogon gouinii</i>	+M	0.621 ^a \pm 0.27	0.273 ^a \pm 0.06	2.14 ^a \pm 0.5	0.669 ^a \pm 0.067	0.33 ^a \pm 0.05	0.047 ^a \pm 0.001
	-M	0.047 ^b \pm 0.026	0.058 ^b \pm 0.057	1.15 ^b \pm 0.5	0.499 ^b \pm 0.12	0.50 ^b \pm 0.11	0.032 ^b \pm 0.007
<i>Panicum purpurascens</i>	+M	0.027 ^a \pm 0.01	0.135 ^a \pm 0.005	0.26 ^a \pm 0.15	0.198 ^a \pm 0.082	0.801 ^a \pm 0.08	0.032 ^a \pm 0.007
	-M	0.007 ^b \pm 0.002	0.006 ^b \pm 0.001	1.19 ^b \pm 0.5	0.522 ^b \pm 0.10	0.47 ^a \pm 0.10	0.022 ^b \pm 0.002

Table 3 Leaf area (LA) (cm²), Leaf number (LN), Specific leaf area (SLA) (cm² g⁻¹), Leaf area ratio (LAR) (cm² g⁻¹) and Net assimilation rate (NAR) (g cm² day⁻¹) of 63 day-old mycorrhizal (+M) and non-mycorrhizal (-M) plants of different species distributed un a tropical sand dune ecosystem on the Gulf of Mexico. Bold numbers are the range of leaf number. Data represent the average \pm standard error of seven replicates. Different letters indicate statistically significant difference between mycorrhizal and non-mycorrhizal treatment according to the student's *t*-test ($p < 0.05$).

		LA	LN	SLA	LAR	NAR
<i>Canavalia rosea</i>	+M	313.2 ^a \pm 36.4	6 ^a \pm 0.8	240.5 ^a \pm 22.6	105.6 ^a \pm 12.4	0.0006 ^a \pm 0.0001
	- M	181.8 ^b \pm 35.2	4 ^b \pm 0.8	190.8 ^b \pm 10.8	82.5 ^b \pm 8.5	0.0007 ^a \pm 0.0005
<i>Ipomoea pes-caprae</i>	+M	48.5 ^a \pm 11.9	7 ^a \pm 1	124.9 ^a \pm 10.5	28.8 ^a \pm 4.8	0.0006 ^a \pm 0.0001
	- M	45.7 ^a \pm 7.6	8 ^a \pm 2	125.4 ^a \pm 8.9	25.6 ^a \pm 2.9	0.0006 ^a \pm 0.0008
<i>Chamaecrista. chamaecristoides</i>	+M	38.8 ^a \pm 8.7	19 ^a \pm 4	330.3 ^a \pm 34.2	101.8 ^a \pm 17.1	0.0007 ^a \pm 0.0006
	- M	6.5 ^b \pm 1.6	7 ^b \pm 2	250.4 ^b \pm 34.2	75.5 ^b \pm 11.1	0.0006 ^a \pm 0.0001
<i>Palafoxia lindenii</i>	+M	15.7 ^a \pm 1.9	10 ^a \pm 1	343.5 ^a \pm 16.3	123.9 ^a \pm 18.6	0.0006 ^a \pm 0.0009
	- M	3.7 ^b \pm 1.3	5 ^b \pm 1	241.1 ^b \pm 18.9	79.2 ^b \pm 16.6	0.0006 ^a \pm 0.0001
<i>Sporobolus virginicus</i>	+M	22.3 ^a \pm 5	12 ^a \pm 2	---	72.4 ^a \pm 18.2	---
	- M	15.3 ^b \pm 3.8	10 ^a \pm 3	---	65.4 ^a \pm 14.9	---
<i>Trachypogon gouinii</i>	+M	27.7 ^a \pm 5.3	10 ^a \pm 1	---	36.2 ^a \pm 11.9	---
	- M	4.0 ^b \pm 1.8	4 ^b \pm 1	---	58.0 ^a \pm 39.3	---
<i>Panicum purpurascens</i>	+M	22.4 ^a \pm 14.8	8 ^a \pm 0.5	---	306.7 ^a \pm 106	---
	- M	2.2 ^b \pm 0.6	4 ^b \pm 0.5	---	166.0 ^a \pm 34.6	---



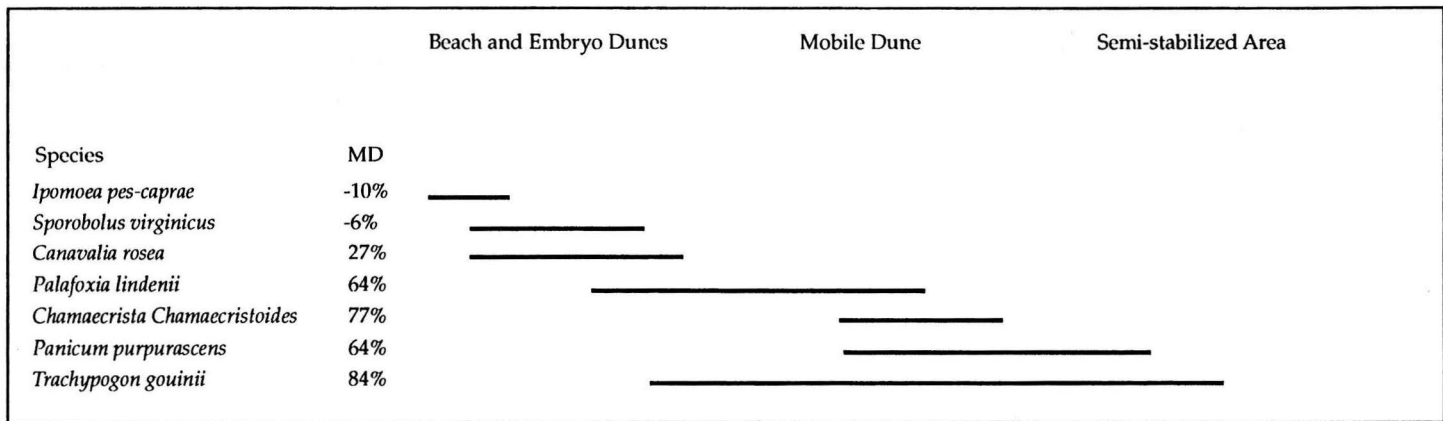


Fig. 2 Mycorrhizal dependency (MD) (according to Plenchette et al. 1983) and distribution of species distributed in the sand dunes at CICOLMA

Discussion

Mycorrhizal responsiveness in different successional stages

Even though in nature "...mycorrhizae have evolved as the norm of terrestrial plant nutrition, not the exception" (Trappe 1977), different species show a great range of responses to the symbiosis with AMF (Plenchette et al. 1983; Habte and Manjunath 1991). Early successional species are typically nonmycorrhizal or facultatively mycorrhizal (Janos 1980), but the growth responses to AM colonization, of all the sand dune species presented in this study, did not correspond exactly to their seral status. Contrasting mycorrhizal responsiveness was demonstrated for the different pioneer species. Therefore, it cannot be concluded that all of them followed the predicted trend of being less responsive to mycorrhizae (Janos 1980; Allen and Allen 1990).

Ipomoea pes-caprae, Canavalia rosea and Sporobolus virginicus are all stoloniferous species which creep over the sand surface and their distribution is restricted to the beach, embryo dunes and foredunes (Moreno-Casasola et al. 1982; Moreno-Casasola and Espejel 1986). Although these species are reported as mycorrhizal in the natural conditions of the sand dunes (Logan et al. 1989; L. Corkidi and E. Rincón submitted), their growth responses could support very clearly the models which state that pioneer species are non-responsive at all or less responsive to mycorrhizae than late seral species (Janos 1980; Allen and Allen 1990). Low responses or similar non-responses to arbuscular mycorrhizae by the genus Ipomoea have also been found in different studies with I. pes-caprae from this tropical sand dune system in La Mancha (Salas 1994; Pérez-Maqueo 1996), I. wolcottiana from a tropical deciduous forest in Mexico (Huante et al. 1993) and I. brasiliensis from Hawaiian sand dunes (Koske and Gemma 1995). However, the longer stems of the mycorrhizal C. rosea

with twice the dry biomass of the nonmycorrhizal plants, could be ecologically significant for a stoloniferous species, even when it was one of the less responsive to the inoculation with the native mycorrhizal fungi. The stem length is an important characteristic of the prostrate growth forms which creep foraging for resources (Bell 1984; Slade and Hutchings 1987), and perhaps particularly when these species are subjected to burial by sand accretion (Moreno-Casasola et al. 1982; Moreno-Casasola 1988).

Palafoxia lindenii and Trachypogon gouinni, can be found in the foredunes, but like Chamaecrista chamaecristoides, they are also very important pioneer species of the mobile areas (Moreno-Casasola 1986; Martínez et al. 1993). The high mycorrhizal response of these species suggests that mycorrhizal infection could also be crucial for the growth and development of early seral species.

Both the beach, embryo dunes and foredunes, as well as the mobile dunes, are sites initially colonized by pioneer species (Davy and Figueroa 1993). However, these areas are influenced by different physical factors and causes of disturbance (Moreno-Casasola et al. 1982; Martínez et al. 1993). Since the beach, embryo dunes and foredunes are closer to the sea, they are subjected to occasional inundation either by sea or freshwater (Pérez-Maqueo 1996). This increases salinity, as well as the contents of Ca and Mg and produces a pH of 8.7 to 8.8. Although the mobility of sand is lowered close to the drift line by the high soil moisture, the plants which grow towards the embryo dunes and foredunes are frequently subjected to burial by sand accretion (Moreno-Casasola et al. 1982). In turn, the strong winds and lower plant density produce a higher degree of sand mobility in the mobile area. This area is also characterized by the extremely low contents of organic matter (0 to 0.7%) and the high temperature fluctuations on the soil surface (Moreno-Casasola 1982; Moreno-Casasola et al. 1982).

Considering the effects of mycorrhizae on the growth of the species discussed above, plants with very different mycorrhizal responsiveness interact at the beach, embryo dunes and foredunes. However, it is interesting to observe that *I. pes-caprae*, the least responsive species, is the most tolerant species to inundation conditions (Pérez-Maqueo 1996) and the one which can be found closer to the drift line, an area subjected to high disturbance and higher nutrient concentrations (Read 1989; Allen and Allen 1990; Pérez-Maqueo 1996). Moreover, it has been reported that inoculation with AMF caused a high mortality percentage in plants of *P. lindenii* and *C. rosea* when they were subjected to flooding conditions (Pérez Maqueo 1995).

In spite of the lower mycorrhizal inoculum potential reported in the mobile dunes, there is a high percentage of mycorrhizal species (L. Corkidi and E. Rincón, submitted), with high mycorrhizal responsiveness. The fact that *C. chamaecristoides* shows colonization by AMF in the mobile dunes, and has high mycorrhizal response, could be of considerable ecological significance. This species is an endemic low shrub of the sand dunes of Mexico, which is highly tolerant to sand accretion, erosion, very poor nutrient levels and drought (Moreno-Casasola 1986; Martínez and Rincón 1993; Martínez et al. 1994). It is the first colonizing plant in areas of intense sand movement on the windward and the leeward slopes and arms and crests of the mobile dunes in which it tends to be the most important stabilizing element (Moreno-Casasola and Espejel 1986). Once *C. chamaecristoides* is established, other species, such as *T. gouinii*, *P. purpurascens*, *P. lindenii* or *Schizachyrium* sp. appear. Interestingly, the species that are able to establish themselves after the colonization of *C. chamaecristoides*, were as responsive to mycorrhizae as this plant or more. Allen and Allen (1980) have reported that although mycorrhizal colonization is severely reduced after disturbance, in an early successional habitat, the infection percentage as well as spore number increases when mycotrophic plants are present.

T. gouinii and P. purpurascens, the species which persist up to the semi-stabilized areas were among the most responsive species to the arbuscular mycorrhizal treatment. P. purpurascens mycorrhizal plants which were followed up to 120 days after transplanting, had spikes, while the nonmycorrhizal were dying (L. Corkidi, unpublished results). Similar high responses of plants to the association with arbuscular mycorrhizal fungi have been produced by late seral species from this tropical sand dune system. While Macroptilium atropurpureum, Crotalaria incana and Tecoma stans increased considerably their growth parameters, Pectis sarejoides produced flowers when mycorrhizal but could not survive when non-mycorrhizal (L. Corkidi unpublished results).

Effects of arbuscular mycorrhizae on relative growth rate, net assimilation rate and biomass allocation

In coastal sand dune systems pioneer plants are subjected to considerable stress from the scarcity of nitrogen, phosphorus, potassium and organic matter, as well as from the low water availability (Moreno-Casasola 1982; Maun 1994). Therefore, it would be expected that in these ecosystems the plant species would grow relatively slowly and allocate a larger fraction of biomass to their roots, increasing their root/shoot ratios (Chapin 1980; Chapin 1988; Lambers and Poorter 1992).

The low growth rates found in the mycorrhizal and nonmycorrhizal sand dune species used in this study coincide with the low growth rates which have been obtained for C. chamaecristoides, Canavalia rosea, Ipomoea pes-caprae, Trachypogon gouinii, Palafoxia lindeni and Schizachyrium scoparium even under rich nutrient treatments (Martínez and Rincón 1993; Valverde et al. 1996) and with no water stress (Martínez et al. 1994; A. Díaz Ortega, personal communication).

The non-significant differences between mycorrhizal and nonmycorrhizal treatments in the net assimilation rate in all the species included in this study, suggest that the mycorrhizal association was not influencing the plant growth through a higher biomass gain per unit leaf area. However, since the relative growth rate is linearly related also to the leaf area ratio ($RGR = NAR \times LAR$) (Lambers and Poorter 1992), the increases in the other parameters related to leaf area were considered more important, as shown by the greater leaf areas, leaf numbers, leaf area ratios and specific leaf areas as well (even in some of the less responsive species).

Regarding the biomass allocation, it must be considered that very different growth forms (stoloniferous, rhizomatous, short shrubs) were included in the experiment. Therefore, the high root/shoot ratios expected in species from sites which are poor in nutrients cannot be generalized to the plants distributed in this sand dune ecosystem. Most of the species allocated the same amount or more of dry biomass to the aerial than to the below-ground part of the plant. Moreover, with the exception of some of the members of the Gramineae family, it seems that the mycorrhizal treatment did not change the general pattern of allocation. In *P. lindenii*, *S. virginicus* and *C. rosea*, although the higher allocation to the aerial part of the plant remained unchanged in the mycorrhizal and the non-mycorrhizal plants, there was certain trend to increase the root weight ratio in the plants which were not inoculated with AMF. Although the difference between treatments was not statistically significant in *P. lindenii*, the increase in the RWR values obtained in the other two species, was significant. In the case of *C. rosea*, the increase in the root weight ratio in nonmycorrhizal plants could explain the absence of difference between inoculated and non-inoculated plants in the root dry biomass. The higher allocation to the aerial part than to the root in *C. rosea* has been supported by other studies in which this species has been grown under situations of competition (Salas 1994), flooding with freshwater and saltwater (Pérez-

Maqueo 1995) and nutrient-rich regimes (Valverde et al. 1996). This is also the general pattern of allocation shown by other clonal species, which has been reported in previous studies (Slade and Hutchings 1987).

The significant increase in the root/shoot ratio of the non-mycorrhizal Panicum purpurascens could be due to the severe reduction in the leaf area and leaf number in the plants that were not inoculated.

The high mycorrhizal status found in all the coastal sand dunes species that have been surveyed throughout the world (e.g. Giovannetti 1985; Puppi and Riess 1987; Koske 1988; Koske and Halvorson 1989; Logan et al. 1989), the influence of mycorrhizal fungi in the stabilization of these ecosystems by binding sand grains into aggregates (Koske et al. 1975; Sutton and Sheppard 1976; Clough and Sutton 1978; Forster 1979; Forster and Nicolson 1981a, b), as well as the studies about the dispersion of arbuscular mycorrhizae in Hawaii (Koske and Gemma 1990), are part of the findings that have supported the statement by Webley et al. (1952), quoted at the beginning of this paper. The range of mycorrhizal responsiveness found in the different pioneer species could be added as further important evidence.

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References

- Abe JP, Masuhara G, Katsuya K (1994) Vesicular-arbuscular mycorrhizal fungi in coastal dune plant communities. I. Spore formation of Glomus spp. predominates under a patch of Elymus mollis. *Mycoscience* 35:233-238
- Abe JP, Katsuya K (1995) Vesicular-arbuscular mycorrhizal fungi in coastal dune plant communities. II. Spore formation of Glomus spp. predominates under geographically separated patches of Elymus mollis. *Mycoscience* 36:113-116
- Allen EB, Allen MF (1980) Natural re-establishment of vesicular-arbuscular mycorrhizae following stripmine reclamation in Wyoming. *J Appl Ecol* 17:139-147
- Allen EB, Allen MF (1990) The mediation of competition by mycorrhizae in successional and patchy environments. In: Grace JB, Tilman GD (eds) *Perspectives on plant competition*. Academic Press, New York, pp 367-389
- Allen MF (1987) Re-establishment of mycorrhizas on Mount-St Helens: migration vectors. *Trans Br Mycol Soc* 88:413-417
- Allen MF (1988) Re-establishment VA of mycorrhizae following severe disturbance: comparative patch dynamics of a shrub desert and a subalpine volcano. *Proc Roy Soc Edinburgh* 94B:63- 71
- Allen MF (1991) *The ecology of mycorrhizae*. Cambridge University Press
- Allen MF, MacMahon JA, Andersen DC (1984) Reestablishment of Endogonaceae on Mount St Helens: Survival of residuals. *Mycologia* 76:1031-1038
- Blaszkowski J (1994) Arbuscular fungi and mycorrhizae (Glomales) of the Hel Peninsula, Poland. *Mycorrhiza* 5:71-88
- Bell AD (1984) *Dynamic morphology: A contribution to plant population ecology*. In: Dirzo R, Sarukhán J (eds) *Perspectives on plant population ecology*. Sinauer Associates Inc, Massachusetts, pp 48-65

- Causton DR, Venus JC (1981) *The biometry of plant growth*. Edward Arnold, London
- Chapin FS (1980) The mineral nutrition of wild plants. *Ann Rev Ecol Syst* 11:233-260
- Chapin FS (1988) Ecological aspects of plant mineral nutrition. *Adv Min Nut* 3:161-191
- Clough KS, Sutton JC (1978) Direct observation of fungal aggregates in sand dune soil. *Can J Microbiol* 24:333-335
- Dalpe Y (1989) Inventaire et répartition de la flore endomycorrhizienne de dune et de rivages maritimes du Québec, du Nouveau Brunswick et de la Nouvelle-Ecosse. *Nat Can* 116:219-236
- Davy AJ, Figueroa ME (1993) The colonization of strandlines. In: Miles J, Walton DWH (eds) *Primary succession on land*. Blackwell Scientific Publications, Oxford, pp:113-131
- Dominik T (1951) Badania mykotrofizmu roslinnosci wydm nadmorskich i srodladowyck. *Acta Soc Bot Pol* 21:125-164
- Dubroeuq D, Geissert D, Moreno-Casasola P, Millot G (1992) Soil evolution and plant communities in coastal dunes near Veracruz, Mexico. *Cah Orstom, sér Pédol XXVII* : 237-250
- Evans GC (1972) *The quantitative analysis of plant growth*. Blackwell Sci Pub, Great Britain
- Forster SM (1979) Microbial aggregation of sand in an embryo dune system. *Soil Biol Biochem* 11:537-543
- Forster SM, Nicolson TH (1981a) Microbial aggregation of sand in a maritime sand dune succession. *Soil Biol Biochem* 13:205-208
- Forster SM, Nicolson TH (1981b) Aggregation of sand from a maritime embryo sand dune by microorganisms and higher plants. *Soil Biol Biochem* 13:199-203

- Gemma JN, Koske RE (1988) Seasonal variation in spore abundance and dormancy of Gigaspora gigantea and in mycorrhizal inoculum potential of a dune soil. *Mycologia* 80:211- 216
- Gemma JN, Koske RE (1989) Field inoculation of American beachgrass (Ammophila breviligulata) with V-A mycorrhizal fungi. *J Environ Manag* 29:173-182
- Gemma JN, Koske RE (1992) Are Mycorrhizal Fungi present in early stages of primary succession In: Read DJ, Lewis DH, Fitter AH, Alexander IJ (eds) *Mycorrhizas in ecosystems*. CAB international, University Press, Cambridge, pp 183-189
- Giovannetti M (1985) Seasonal variations of vesicular arbuscular mycorrhizas and Endogonaceous spores in a maritime sand dune. *Trans Br Mycol Soc* 84:679-684
- Giovannetti M, Nicolson TH (1983) Vesicular-arbuscular mycorrhizas in Italian sand dunes. *Trans Br Mycol Soc* 80:552-557
- Habte M, Manjunath A (1991) Categories of vesicular-arbuscular mycorrhizal dependency of host species. *Mycorrhiza* 1: 3-12
- Huante P, Rincón E, Allen EB (1993) Effect of vesicular-arbuscular mycorrhizae on seedling growth of four tree species from the tropical deciduous forest in Mexico. *Mycorrhizae* 2:141-145
- Hunt R (1982) *Plant growth curves: The functional approach to plant growth analysis*. Edward Arnold, London
- Janos DP (1980) Mycorrhizae influence tropical succession. *Biotropica* 12:56-64
- Kellman M, Roulet N (1990) Nutrient flux and retention in a tropical sand-dune succession. *J Ecol* 78:664-676
- Koide RT, Li M (1989) Appropriate controls for vesicular-arbuscular mycorrhiza research. *New Phytol* 111:35-44

- Koske RE (1988) Vesicular-arbuscular mycorrhizae of some Hawaiian dune plants. *Pacific Sci* 42:217-229
- Koske RE, Sutton JC, Sheppard BR (1975) Ecology of *Endogone* in Lake Huron sand dunes. *Can J Bot* 53:87-93
- Koske RE, Halvorson WL (1981) Ecological studies of vesicular-arbuscular mycorrhizae in a barrier sand dune. *Can J Bot* 59:1413-1422
- Koske RE, Polson WR (1984) Are VA mycorrhizae required for sand dune stabilization? *Bioscience* 34:420-424
- Koske RE, Gemma JN (1989) A modified procedure for staining roots to detect VA mycorrhizas. *Mycol Res* 92:486-488
- Koske RE, Halvorson (1989) Mycorrhizal associations of selected plant species from San Miguel Island, Channel Islands National Park, California. *Pacific Sci* 3:32-40
- Koske RE, Gemma JN (1990) VA mycorrhizae in strand vegetation of Hawaii: Evidence for long distance codispersal of plants and fungi. *Amer J Bot* 77:466-474
- Koske RE, Gemma JN (1995) VA mycorrhizal inoculation of Hawaiian plants: A conservation technique for endangered tropical species. *Pacific Sci* 49:181-191
- Lambers H, Poorter H (1992) Inherent variation in growth rate between higher plants: A search for physiological causes and ecological consequences. *Adv Ecol Res* 23:187-261
- Logan VS, Clarke PJ, Allaway WG (1989) Mycorrhizas and root attributes of plants of coastal sand-dunes of New South Wales. *Aust J Plant Physiol* 16:141-146
- Martínez ML, Valverde T, Moreno-Casasola P (1992) Germination response to temperature, salinity, light and depth of sowing of ten tropical dune species. *Oecologia* 92: 343-353

- Martínez ML, Moreno-Casasola P, Castillo S (1993) Biodiversidad Costera: Playas y dunas. In: Salazar-Vallejo SI, González NE (eds) Biodiversidad marina y costera de México, Com Nal Biodiversidad y CIQRO, México, pp 160-181
- Martínez ML, Moreno-Casasola P, Rincón E (1994) Sobrevivencia y crecimiento de plántulas de un arbusto endémico de dunas costeras ante condiciones de sequía. *Acta Bot Mex* 26:53-62
- Martínez ML, Rincón E (1993) Growth analysis of Chamaecrista chamaecristoides (Leguminosae) under contrasting nutrient conditions. *Acta Oecol* 14:521-528
- Martínez ML, Moreno-Casasola P (1995) Effects of burial by sand on seedling growth and survival in six tropical sand dune species from the Gulf of Mexico. *J Coastal Res*
- Maun MA (1994) Adaptations enhancing survival and establishment of seedlings on coastal dune systems. *Vegetatio* 111:59-70
- Miller RM (1979) Some occurrences of vesicular-arbuscular mycorrhizae in natural and disturbed ecosystems of the Red Desert. *Can J Bot* 57:619-623
- Miller RM (1987) Mycorrhizae and succession. In: Jordan III WR, Gilpin ME, Aber JD (eds) *Restoration ecology. A synthetic approach to ecological research*. Cambridge University Press, Cambridge, pp:205-220
- Moreno-Casasola P (1982) Ecología de la vegetación de dunas costeras: Factores físicos. *Biotica* 7:577-602
- Moreno-Casasola P (1986) Sand movement as a factor in the distribution of plant communities in a coastal dune system. *Vegetatio* 65:67-76
- Moreno-Casasola P (1988) Patterns of plant species distribution on coastal dunes along the Gulf of Mexico. *J Biogeogr* 15:787-806

- Moreno-Casasola P, van der Maarel E, Castillo S, Huesca ML, Pisanty I (1982) Ecología de la vegetación de dunas costeras: Estructura y composición en el Morro de la Mancha, Ver. *Biotica* 7:491-526
- Moreno-Casasola P and Espejel I (1986) Classification and ordination of coastal sand dune vegetation along the Gulf and Caribbean sea of Mexico. *Vegetatio* 66:147-182
- Nicolson TH (1960) Mycorrhizae in the Gramineae. II. Development in different habitats particularly sand dunes. *Trans Br Mycol Soc* 43:132-145
- Nicolson TH, Johnston C (1979) Mycorrhiza in the Gramineae III. Glomus fasciculatus as the endophyte of pioneer grasses in a maritime sand dune. *Trans Br Mycol Soc* 72: 261-268
- Pendleton RL, Smith BN (1983) Vesicular-arbuscular mycorrhizae of weedy and colonizer plant species at disturbed sites in Utah. *Oecologia (Berl)* 59:296-301
- Pérez Maqueo O (1995) Análisis del efecto de los disturbios en la dinámica de la playa del Morro de la Mancha, Veracruz. M. Sc. Thesis, UNAM, Mexico
- Plenchette C, Fortin JA, Furlan V (1983) Growth responses of several plant species to mycorrhiza in a soil of moderate P fertility. I. Mycorrhizal dependency under field conditions. *Plant Soil* 70:191-209
- Puppi G, Riess S (1987) Role and ecology of VA Mycorrhizae in sand dunes. *Angew Bot* 61:115-126
- Read DJ (1989) Mycorrhizas and nutrient cycling in sand dune ecosystems. *Proc Roy Soc Edinburgh* 96B:89-100
- Reeves FB, Wagner DW, Moorman T, Kiel J (1979) The role of endomycorrhizae in revegetation practices in the semi-arid west. I. A comparison of incidence of mycorrhizae in severely disturbed vs. natural environments. *Amer J Bot* 66: 1-13

- Rovira AD, Bowen GD (1966) The effects of microorganisms upon plant growth. II. Detoxication of heat-sterilized soils by fungi and bacteria. *Plant Soil* 25:129-141
- Salas M (1994) Efecto de las micorrizas vesículo-arbusculares en la competencia por nutrimentos entre dos especies pioneras de dunas costeras del Morro de la Mancha, Veracruz. B Sc Thesis, UNAM, Mexico
- Schmidt SK, Scow KM (1986) Mycorrhizal fungi on the Galapagos Islands. *Biotropica* 18:236-240
- Slade AJ, Hutchings MJ (1987) Clonal integration and plasticity in foraging behaviour in *Glechoma hederaceae*. *J Ecol* 75:1023-1036.
- Stahl E (1900) Der Sinn der Mycorrhizenbildung. *Jahrbucher für wissenschaftliche Botanik* 34:539-668
- Sturmer SL, Bellei MM (1994) Composition and seasonal variation of spore populations of arbuscular mycorrhizal fungi in dune soils on the island of Santa Catarina, Brazil. *Can J Bot* 72:359-363
- Sutton JC, Sheppard BR (1976) Aggregation of sand dune soil by endomycorrhizal fungi. *Can J Bot* 54:326-333
- Trappe JM (1977) Selection for fungi for ectomycorrhizal inoculation in nurseries. *Ann Rev Phytopathol* 15:203-222
- Valverde T, Pisanty I, Rincón E (1996) Growth response of six tropical dune plant species to different nutrient regimes. *J Coastal Res* 12: 000-000
- Webley DM, Eastwood DJ, Gimingham CH (1952) Development of a soil microflora in relation to plant succession on sand-dunes, including the rhizosphere flora associated with colonizing species. *J Ecol* 40:168-178
- Willis AJ, Yem EW (1961) Braunton Burrows: Mineral nutrient status of the dune soils. *J Ecol* 49:377-390

Zar JH (1974) Biostatistical Analysis. Prentice Hall, London

5) Discusión general

Las dunas son muy importantes como barreras naturales para la protección de las costas contra mareas altas y huracanes, sitios de interés ecológico, así como áreas de recreación. Por lo tanto, se ha considerado la necesidad de idear estrategias apropiadas para su manejo y conservación (van der Muelen 1990; van der Putten 1990; Martínez et al. 1993). Para ello, se ha propuesto mantener la heterogeneidad ambiental y la dinámica espacio-temporal preservando todos los estadios sucesionales (van der Muelen 1990; Martínez et al. 1993).

La morfología de los sistemas de dunas, incluyendo tanto la forma de las dunas individuales como el arreglo espacial de los complejos de dunas, depende de varios factores, entre los que se encuentran, la morfología de la playa, las características del viento (fuerza, frecuencia y dirección), el grado y crecimiento de la cobertura vegetal y las actividades humanas (Pye 1990). Desde los estudios clásicos que realizó Cowles de 1896 a 1898, en las dunas de Michigan, ya se reconocía el papel de las plantas colonizadoras en el control del movimiento de arena y en la estabilización de estos ecosistemas (Cowles 1899; Willis et al. 1959; Koske & Polson 1984; Will & Sylvia 1990). De hecho, uno de los medios principales de restauración de las costas del Atlántico en Norte América, es la introducción de Ammophila breviligulata (Zak 1965), de Uniola paniculata o de diferentes especies de Panicum (Will & Sylvia 1990).

Webley et al. (1952) determinaron el número de hongos y bacterias asociados a la rizósfera de plantas de distintos estadios serales en las dunas costeras de Inglaterra y propusieron que la actividad de los microorganismos del suelo es uno de los factores bióticos que contribuyen de manera determinante en la sucesión de estos ecosistemas. Los resultados que se han obtenido, a partir de los estudios realizados sobre asociaciones micorrícicas arbusculares en dunas costeras, también han apoyado esta hipótesis. Entre éstos se pueden mencionar: El alto porcentaje de especies micorrícicas que se encuentra en

la mayor parte de los sistemas de dunas (Giovannetti & Nicolson 1983; Giovannetti 1985; Peterson et al. 1985; Logan et al. 1989; Koske 1988; Koske & Gemma 1990); la influencia de las hifas de los hongos micorrícicos en la estabilización de estos ecosistemas al unir los granos de arena y formar agregados más resistentes al viento (p. ej. Koske et al. 1975; Sutton & Sheppard 1976; Forster & Nicolson 1979, 1981a, b) y los estudios que demuestran la dispersión y viabilidad de esporas junto con los propágulos vegetativos de algunas especies desde las líneas de mareas (Nicolson 1960; Koske & Gemma 1990).

A partir de la descripción de la condición micorrícica de especies distribuidas en distintas zonas de las dunas, del potencial de inóculo de la arena y de la comparación del crecimiento de plantas en presencia y ausencia de asociaciones micorrícicas, esta tesis también aporta evidencias respecto al posible significado ecológico de las micorrizas arbusculares en los ecosistemas de dunas. Anteriormente se han realizado algunos trabajos que reportan los efectos de las micorrizas en el crecimiento de plantas de dunas (Nicolson & Johnston 1979; Gemma & Koske 1989; Sylvia & Burk 1988; Will & Sylvia 1990). Sin embargo, en ninguno se compara la respuesta de varias especies que se establecen durante la primera etapa de la colonización de diferentes zonas de este sistema. Tampoco se analiza con detalle la influencia de las micorrizas en los diferentes parámetros del crecimiento de las plantas, ni se reporta el efecto de la simbiosis en la asignación de biomasa.

Micorrizas arbusculares en el sistema de dunas del Centro de Investigaciones Costeras de La Mancha

Condición micorrícica

De acuerdo con la presencia de hifas, vesículas, enrollamientos hifales o arbusculos, el 97% de las especies que se colectaron en la playa y en las diferentes zonas sucesionales en el sistema de dunas costeras de la Mancha, se reportaron como micorrícicas. Este porcentaje, es consistente con el alto número de especies micorrícicas que se ha reportado en otros sistemas de dunas, tanto de zonas templadas como sub-tropicales (Koske et al. 1975; Giovannetti & Nicolson 1983; Giovannetti 1985; Peterson et al. 1985; Puppi et al. 1986; Puppi & Riess 1987; Koske 1988; Dalpé 1989; Koske & Halvorson 1989; Logan et al. 1989; Koske & Gemma 1990). Sería importante señalar que más del 50% de las especies de la Mancha que se analizaron, presentaron hifas y vesículas pero no arbusculos, lo cual se considera importante para determinar si la asociación micorrícica es funcional o no. Sin embargo, cabe mencionar que las colectas fueron muy puntuales y también que sería conveniente utilizar un mayor número de muestras.

Porcentajes de colonización micorrícica y potencial de inóculo de la arena de la playa, duna móvil, pastizal de Trachypogon gouinii y matorral de Dyphisa robinoides

En los estudios realizados en las dunas de Europa y Norte América, se ha encontrado que el porcentaje de colonización por hongos micorrícicos varía respecto a la estación del año y la posición en este tipo de ecosistemas (Nicolson 1960; Nicolson & Johnston 1979; Jehne & Thompson 1981; Giovannetti 1985; Puppi et al. 1986; Sylvia 1986; Gemma & Koske 1988; Mohankumar et al. 1988). Por lo tanto, se esperaba cierta tendencia a obtener mayores potenciales de inóculo y mayores valores de colonización micorrícica, en las plantas colectadas en zonas estabilizadas (pastizal y matorral) en

comparación con las de zonas de pioneras (playa y duna móvil). Por medio del experimento del potencial de inóculo micorrícico, se comprobó la diferencia entre los porcentajes de colonización provenientes de sustratos de diferentes zonas sucesionales. Los resultados indicaron que la zona del matorral y del pastizal tienen potenciales de inóculo significativamente mayores que la zona móvil. Estos resultados son consistentes con los que obtuvieron Nicolson (1960), Nicolson & Johnston (1979) y Koske & Polson (1984). La información obtenida a partir de sus estudios sugiere, que tanto la colonización por hongos micorrícicos arbusculares, así como su micelio externo y el número de esporas que producen, aumenta conforme se incrementa la densidad de especies y la estabilidad de las dunas. Los porcentajes de colonización que se obtuvieron en la zona de la playa no fueron significativamente menores que los de una de las zonas estabilizadas (pastizal). Es importante notar, que la arena de la zona de la playa que se utilizó para este experimento se colectó alrededor de la rizósfera de un parche formado por plantas de Palafoxia lindenii, una especie con altos valores de colonización micorrícica. El potencial de inóculo obtenido, podría relacionarse con la mayor densidad de especies que se encontraba en esta zona y probablemente, a la ausencia de disturbios recientes en el momento de la colecta.

Los porcentajes de colonización micorrícica de Trachypogon gouinii que se obtuvieron en las zonas de pioneras, móvil y pastizal no fueron diferentes estadísticamente. En principio, existe una alta variación entre las muestras. Por lo tanto es difícil sacar conclusiones al respecto.

Sería importante cuestionar, cuál es el valor del cálculo del porcentaje de colonización por hongos micorrícicos arbusculares como un método confiable, en raíces obtenidas en sistemas naturales, y cuál es su significado ecológico. En otros estudios en donde se han determinado los valores de colonización, también se han obtenido intervalos muy amplios de variación entre las muestras (ej. Giovannetti & Nicolson 1983; Giovannetti 1985). Existe una gran probabilidad de error en el muestreo, debido en gran parte a la dificultad de obtener muestras al azar de la raíz en los ejemplares del campo. Por otra parte,

no se conoce el tiempo de producción de las raíces que se están muestreando, por lo tanto las estructuras micorrícicas observadas pueden pertenecer a raíces producidas en estaciones anteriores. Considerando el efecto de los porcentajes de colonización en el crecimiento de las plantas, el incremento en la biomasa no siempre está relacionado con un incremento en la colonización por hongos arbusculares (Daft & Nicolson 1969; Clapperton & Reid 1992). Adicionalmente, la efectividad del inóculo puede estar determinada tanto por la abundancia de propágulos, como por la identidad de las especies y la viabilidad de las estructuras que producen (Abbot & Robson 1978; Sylvia & Burks 1988).

El conocimiento del patrón estacional de la colonización podría ser de interés considerable si se relacionara con la fenología de la planta. Los periodos durante los cuales hay porcentajes de colonización altos, pueden estar relacionados tanto con la influencia de las micorrizas en el estado nutricional de las plantas como en las demandas de carbono del hongo (Sanders & Fitter 1992).

Las micorrizas arbusculares en la primera etapa del crecimiento de plantas pioneras de las dunas de la Mancha

Por medio del experimento de crecimiento, se comprobó que ante situaciones ambientales semejantes, siete especies que se establecen durante la primera etapa de colonización de diferentes zonas de las dunas, presentaron distintas respuestas a la inoculación con hongos micorrícicos arbusculares.

En la playa y dunas embrionarias se encuentran interactuando plantas con muy diferentes respuestas a la asociación micorrícica, en cuanto a su producción de biomasa. Ipomoea pes-caprae, Canavalia rosea y Sporobolus virginicus son especies estoloníferas rastreras cuya distribución está restringida a la playa, dunas embrionarias y frontales (Moreno-Casasola et al. 1982; Moreno-Casasola & Espejel 1986; Moreno-Casasola 1988). Sin embargo, sus respuestas de crecimiento apoyan los modelos que proponen que las

especies pioneras son facultativamente micorrícicas o no micorrícicas (Janos 1980). La asociación con hongos micorrícicos arbusculares en I. pes-caprae, no provocó ningún incremento en todos los parámetros de crecimiento que se analizaron. Esta respuesta ha sido reportada también en otros experimentos realizados con la misma especie (Salas 1994; Pérez-Maqueo 1996). I. pes-caprae es una de las especies que llega más cerca de la línea de mareas y la más tolerante a las condiciones de inundación que pueden presentarse en la playa (Pérez Maqueo 1996). En otros sistemas de dunas, se ha reportado que las zonas cercanas a las líneas de mareas están colonizadas predominantemente por especies anuales no-micotróficas (Nicolson 1960; Giovannetti & Nicolson 1983; Giovannetti 1985). Esto se ha relacionado tanto con la alta perturbación que sufren estas áreas (Read 1989) como al hecho de que pueden ser más ricas en nutrientes (Allen & Allen 1990).

El incremento en la producción de biomasa de las plantas micorrícicas de C. rosea no fue tan alto. Sin embargo, se observó que la simbiosis puede alterar parámetros del crecimiento que pueden influir en el éxito de esta especie, como es el caso del incremento en el área y el peso foliar y el largo del tallo en especies rastreras tolerantes a factores como enterramiento por la arena.

Palafoxia lindenii, Chamaecrista chamaecristoides y Trachypogon gouinii, pueden encontrarse tanto en la zona de las dunas embrionarias como en la zona móvil. Los altos índices de respuesta micorrícica de estas especies podrían indicar que la asociación con hongos arbusculares micorrícicos también puede ser crucial para las plantas que se establecen desde las primeras etapas de colonización de un ecosistema.

El hecho de que C. chamaecristoides en condiciones naturales se reporte como micotrófica y presente beneficios en su crecimiento cuando está asociada con hongos micorrícicos arbusculares, puede ser de considerable significado ecológico. Esta especie es la primer colonizadora de las dunas móviles (Martínez 1994), es altamente tolerante al enterramiento, a condiciones de sequía y a bajos niveles de nutrientes (Moreno-Casasola 1986; Martínez & Rincón 1993; Martínez et al. 1994; Valverde et al. en prensa). Una vez

que se establece, otras especies pueden colonizar ese sitio (Martínez 1994). Todas las especies que llegan después que C. chamaecristoides, presentaron índices de respuesta micorrícica iguales o mayores que ella. Los resultados obtenidos acerca de la velocidad de infección en la duna móvil indicaron una probabilidad muy baja de infección en la zona donde no hay vegetación. Sin embargo, las plántulas de Panicum purpurascens que se colectaron cerca de C. chamaecristoides sí estaban colonizadas por hongos micorrícicos arbusculares. Debido a que los fuertes vientos que provienen del norte, ocasionan grandes movimientos de arena (Moreno-Casasola 1982), se esperaría que la red de hifas que se considera importante como fuente natural de inóculo no existiera o se destruyera en la zona de dunas móviles. Allen & Allen (1980) reportaron que aunque tanto el porcentaje de colonización como el número de esporas, se reducen considerablemente después de una perturbación, ambos se incrementan cuando hay especies micotróficas presentes. Sería muy interesante investigar de donde viene el inóculo micorrícico que se está asociando con las especies de esta zona tan perturbada y la influencia de la vecindad de los matorrales, de la selva y del viento en la dispersión de las esporas de hongos micorrícicos.

En otros experimentos realizados en condiciones controladas, en donde se investiga el efecto de las micorrizas arbusculares en el crecimiento, también se ha demostrado que las plantas inoculadas incrementan su tasa de crecimiento (Harley & Smith 1983). Sin embargo, los que se han diseñado para investigar la efectividad de la simbiosis en el campo no han sido conclusivos (Fitter 1985). Se ha sugerido que en el campo, los requerimientos de fósforo son muy inconsistentes (Fitter 1985) o pueden ser tan bajos que no se requeriría la ayuda de las micorrizas (Mc Gonigle & Fitter 1988). Sin embargo, parece ser que hay ciertas etapas en el ciclo de vida de las plantas en las cuales la infección micorrícica podría ser importante, como durante el establecimiento de las plántulas o en la floración (Fitter 1991). Por otra parte, también se debe considerar que los beneficios de la asociación micorrícica no sólo pueden estar relacionados con la producción de biomasa. Los resultados de algunas investigaciones sugieren, que las micorrizas podrían jugar un papel importante

en la ecología de la sucesión, ya sea al alterar el resultado de la competencia o al afectar la diversidad de especies (Janos 1980; Allen 1988, Gange et al. 1990, Grime et al. 1987). Por otra parte, también se debe considerar el efecto de la simbiosis en la sobrevivencia (Grime et al. 1987), en la evasión de patógenos (Brundrette 1991; Little & Maun, en prensa), y en el potencial reproductivo de las plantas (Koide et al. 1988).

Desde el "punto de vista" de las plantas, cabe cuestionar en qué momento del ciclo de vida sería "ventajosa" la infección micorrícica. Durante el experimento de crecimiento, en cuatro de las especies utilizadas se realizó una cosecha tres semanas después del trasplante. Para ese momento, las plantas ya estaban asociadas con hongos arbusculares. Sin embargo, no se detectó ninguna diferencia en los parámetros de crecimiento que se analizaron. En experimentos realizados con frijol de soya (Glycine max (L.) Merr), se ha reportado que los primeros periodos de infección ocurren de 10 a 12 días después del trasplante, después de los cuales las unidades de infección se incrementan considerablemente (Carling et al. 1978). Por medio de observaciones visuales sobre la altura de las plántulas, se determinó que las micorrizas empiezan a tener efecto en el crecimiento a partir de la sexta semana.

En el caso de las especies de dunas que se consideraron para este estudio, sería de particular interés realizar estudios con diferentes proporciones de fósforo para determinar la tolerancia de estas especies a los bajos niveles de este recurso. En general, sería importante investigar con detalle el "costo-beneficio" de las asociaciones micorrícicas arbusculares en las diferentes etapas del ciclo de vida de las plantas e investigar el papel de las micorrizas en la etapa de establecimiento de las plántulas.

Bibliografia

- Abbot LK, Robson AD (1978) Growth of subterranean clover in relation to the formation of endomycorrhizas by introduced and indigenous fungi in a field soil. *New Phytol* 81: 575-585
- Allen EB, Allen MF (1980) Natural re-establishment of vesicular-arbuscular mycorrhizae following stripmine reclamation in Wyoming. *J Appl Ecol* 17:139-147
- Allen EB, Allen MF (1990) The mediation of competition by mycorrhizae in successional and patchy environments. In: Grace JB, Tilman GD (eds) *Perspectives on plant competition*. Academic Press, New York, pp:367-389
- Allen MF (1988) Re-establishment VA of mycorrhizae following severe disturbance: Comparative patch dynamics of a shrub desert and a subalpine volcano. *Proc Roy Soc Edinburgh* 94B:63-71
- Birch CPD (1986). Development of VA mycorrhizal infection in seedlings in semi-natural grassland turf. In: Gianinazzi-Pearson V, Gianinazzi S (eds) *Physiological and genetical aspects of mycorrhizae*. Proceedings of the 1st European Symposium on Mycorrhizae. INRA, Paris.
- Carling DE, Brown MF, Brown RA (1979) Colonization rates and growth responses of soybean plants infected by vesicular-arbuscular mycorrhizal fungi. *Can J Bot* 57:1769-1772
- Clapperton MJ, Reid DM (1992) A relationship between plant growth and increasing VA mycorrhizal inoculum density. *New Phytol* 120:227-234
- Clough KS, Sutton JC (1978) Direct observation of fungal aggregates in sand dune soil. *Can J Microbiol* 24:333-335
- Cowles HC (1899) The ecological relations of vegetation on the sand dunes of Lake Michigan. *Bot Gaz* 27:95-117

- Daft MJ, Nicolson TH (1969) Effect of Endogone mycorrhizae on plant growth. III. Influence of inoculum concentration on growth and infection in tomato. *New Phytol* 68:933-963
- Fitter AH (1985) Functioning of vesicular-arbuscular mycorrhizas under field conditions. *New Phytol* 99:257-265
- Fitter AH (1991) Costs and benefits of mycorrhizas: Implications for functioning under natural conditions. *Experientia* 47:350-355
- Forster SM (1979) Microbial aggregation of sand in an embryo dune system. *Soil Biol Biochem* 11:537-543
- Forster SM, Nicolson TH (1981a) Microbial aggregation of sand in a maritime dune succession. *Soil Biol Biochem* 13:205-208
- Forster SM, Nicolson TH (1981b) Aggregation of sand from a maritime embryo sand dune by microorganisms and higher plants. *Soil Biol Biochem* 13:199-203
- Gange AC, Brown VK & Farmer LM 1990. A test of mycorrhizal benefit in an early successional plant community. *New Phytologist* 115:85-91
- Gemma JN, Koske RE (1988) Seasonal variation in spore abundance and dormancy of Gigaspora gigantea and in mycorrhizal inoculum potential of a dune soil. *Mycologia* 80:211-216
- Gemma JN, Koske RE (1989) Field inoculation of American beachgrass (Ammophila breviligulata) with V-A mycorrhizal fungi. *J Environ Manag* 29:173-182
- Gemma JN, Koske RE (1992) Are mycorrhizal fungi present in the early stages of primary succession. In: Read DJ, Lewis DH, Fitter AH, Alexander IJ (eds) *Mycorrhizas in ecosystems*, CAB international, University Press, Cambridge, pp 183-189
- Giovannetti M (1985) Seasonal variations of vesicular-arbuscular mycorrhizas and Endogonaceous spores in a maritime sand dune. *Trans Br Mycol Soc* 84:679-684
- Giovannetti M, Nicolson TH (1983) Vesicular-arbuscular mycorrhizas in Italian sand dunes. *Trans Br Mycol Soc* 80:552-557

- Grime JP, Mackey JM, Hillier SH, Read DJ (1987) Floristic diversity in a model system using experimental microcosms. *Nature* 328:420-422
- Harley, J. L. & S. E. Smith (1983). *Mycorrhizal Symbiosis*. Academic Press, London.
- Janos DP (1980) Mycorrhizae influence tropical succession. *Biotropica* 12:56-64
- Jasper DA, Abbot LK, Robson AD (1989) Soil disturbance reduces infectivity of external hyphae of vesicular arbuscular mycorrhizal fungi. *New Phytol* 112:93-99
- Jehne W, Thompson CH (1981) Endomycorrhizae in plant colonization on coastal sand dunes at Cooloola, Queensland. *Aust J Ecol* 6:221-230
- Mycologia* 79:55-68
- Koide RT, Li M, Lewis J, Irby C (1988) Role of mycorrhizal infection in the growth and reproduction of wild vs. cultivated plants. *Oecologia* 77:537-543
- Koske RE (1988) Vesicular-Arbuscular mycorrhizae of some Hawaiian dune plants. *Pacific Sci* 42:217-229
- Koske RE, Sutton JC, Sheppard BR (1975) Ecology of *Endogone* in Lake Huron sand dunes. *Can J Bot* 53:87-93
- Koske RE, Polson WR (1984) Are VA mycorrhizae required for sand dune stabilization? *Bioscience* 34:420-424
- Koske RE, Gemma JN (1990) VA mycorrhizae in strand vegetation of Hawaii: Evidence for long distance codispersal of plants and fungi. *Amer J Bot* 77:466-474
- Logan VS, Clarke PJ, Allaway WG (1989) Mycorrhizas and root attributes of plants of coastal sand-dunes of New South Wales. *Aust J Plant Physiol* 16:141-146
- McGonigle, T. P. & A. H. Fitter (1988) Ecological consequences of arthropod grazing on VA mycorrhizal fungi. *Proceedings of the Royal Society of Edinburgh* 94B:25-32.
- Martínez ML, Moreno-Casasola P, Castillo S (1993) Biodiversidad Costera: Playas y dunas. In: Salazar-Vallejo SI, González NE (eds) *Biodiversidad marina y costera de México*, Com Nal Biodiversidad y CIQRO, México, pp 160-181

- Martínez ML, Moreno-Casasola P, Rincón E (1994) Sobrevivencia y crecimiento de plántulas de un arbusto endémico de dunas costeras ante condiciones de sequía. *Acta Bot Mex* 26:53-62
- Martínez ML, Rincón E (1993) Growth analysis of Chamaecrista chamaecristoides (Leguminosae) under contrasting nutrient conditions. *Acta Oecol* 14:521-528
- Mc Gonigle TP, Fitter AH (1988) Growth and phosphorus inflows of Trifolium repens L. with a range of indigenous vesicular-arbuscular mycorrhizal infection levels under field conditions. *New Phytol* 108:59-66
- Mohankumar V, Ragupathy S, Nirmala CB, Mahadevan A (1988). Distribution of vesicular arbuscular mycorrhizae (VAM) in the sandy beach soils of Madras Coast. *Current Sci* 57(7):367-368
- Moreno-Casasola P (1982) Ecología de la vegetación de dunas costeras: Factores físicos. *Biotica* 7:577-602
- Moreno-Casasola P (1986) Sand movement as a factor in the distribution of plant communities in a coastal dune system. *Vegetatio* 65:67-76
- Moreno-Casasola P (1988) Patterns of plant species distribution on coastal dunes along the Gulf of Mexico. *J Biogeogr* 15:787-806
- Moreno-Casasola P, van der Maarel E, Castillo S, Huesca ML, Pisanty I (1982) Ecología de la vegetación de dunas costeras: Estructura y composición en el Morro de la Mancha, Ver. *Biotica* 7:491-526
- Moreno-Casasola P and Espejel I (1986) Classification and ordination of coastal sand dune vegetation along the Gulf and Caribbean sea of Mexico. *Vegetatio* 66:147-182
- Nicolson TH (1960) Mycorrhizae in the Gramineae, II. Development in different habitats particularly sand dunes. *Trans Br Mycol Soc* 43:132-145
- Nicolson TH, Johnston C (1979) Mycorrhiza in the Gramineae III. Glomus fasciculatus as the endophyte of pioneer grasses in a maritime sand dune. *Trans Br Mycol Soc* 72:262-268

- Pérez Maqueo O (1996) Análisis dl efecto de los disturbios en la dinámica de la playa del Morro de la Mancha, Veracruz. Tesis de Maestría, Facultad de Ciencias, UNAM, México
- Peterson RL, Ashford AE, Allaway G (1985) Vesicular-arbuscular mycorrhizal associations of vascular plants on Heron Island. A greater barrier coral cay. Aust J Bot 33:669-676
- Plenchette C, Fortin JA, Furlan V (1983) Growth responses of several plant species to mycorrhiza in a soil of moderate P fertility. I. Mycorrhizal dependency under field conditions. Plant Soil 70:191-209
- Puppi G, Tabacchini P, Riess S, Sanvito A (1986) Seasonal patterns in mycorrhizal association in a maritime sand dune system. In: Gianninazzi-Pearson V, Gianninazzi S (eds) Physiological and genetical aspects of mycorrhizae, Paris, INRA pp 245-251
- Puppi G, Riess S (1987) Role and ecology of VA mycorrhizae in sand dunes. Angew Botanik 61:115-126
- Pye, K (1990). Physical and human influences on coastal dune development between the Ribble and Mersey estuaries, northwest England. In: Nordstrom K, Psuty N, Carter B. (eds.). Coastal Dunes. Forms and Process. Ed. John Wiley & Sons. pp. 337-360.
- Read DJ (1989) Mycorrhizas and nutrient cycling in sand dune ecosystems. Proc Roy Soc Edinburgh 96B:89-100
- Salas M (1994) Efecto de las micorrizas vesículo-arbusculares en la competencia por nutrimentos entre dos especies pioneras de dunas costeras del Morro de la Mancha, Veracruz. B Sc Thesis, UNAM, Mexico
- Sanders IR, Fitter AH (1992) The ecology and functioning of vesicular-arbuscular mycorrhizas in co-existing grassland species. I. seasonal patterns of mycorrhizal occurrence and morphology. New Phytol 120:517-524
- Sylvia DM (1986) Spatial and temporal distribution of vesicular-arbuscular mycorrhizal fungi associated with Uniola paniculata in Florida foredunes. Mycologia 78:728-734

- Sylvia DM, Burks JN (1988) Selection of a vesicular arbuscular mycorrhizal fungus for practical inoculation of *Uniola paniculata*. *Mycologia* 80:565-568
- Van der Meulen F (1990) Coastal dune management in the Netherlands. In: Proceedings of the symposium on coastal sand dunes, Guelph University. pp.367-387.
- Van der Putten WH (1990). Establishment and management of *Ammophila arenaria* (Marram grass) on artificial coastal foredunes in the Netherlands. In: Proceedings of the symposium on coastal sand dunes, Guelph University. pp 349-366
- Webley DM, Eastwood DJ, Gimingham CH (1952) Development of a soil microflora in relation to plant succession on sand-dunes, including the rhizosphere flora associated with colonizing species. *J Ecol* 40:168-178
- Will ME, Sylvia DM (1990) Interaction of rhizosphere bacteria, fertilizer, and vesicular arbuscular mycorrhizal fungi with sea oats. *Appl. Environ. Microbiol.*
- Willis AJ (1965) The influence of mineral nutrients on the growth of *Ammophila Arenaria*. *J Ecol* 735-745
- Willis AJ, Folkes BF, Hope-Simon JF, Yemm EW (1959) Branton Burrows: The dune system and its vegetation. *J Ecol* 47:1-24
- Willis AJ, Yemm EW (1961) Branton Burrows: Mineral nutrient status of the dune soils. *J Ecol* 49:377-390