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Comparison of saline tolerance among genetically similar species of *Fusarium* and *Meloidogyne* recovered from marine and terrestrial habitats

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ABSTRACT

Successful plant pathogens co-evolve and adapt to the environmental constraints placed on host plants. We compared the salt tolerance of two salt marsh pathogens, *Fusarium palustre* and *Meloidogyne spartinae*, to genetically related terrestrial species, *F. sporotrichioides* and *Meloidogyne hapla*, to assess whether the salt marsh species had acquired selective traits for persisting in saline environments or if salt tolerance was comparable among *Fusarium* and *Meloidogyne* species. Comparisons of both species were made in vitro in vessels containing increasing concentration of NaCl. We observed that *F. palustre* was more tolerant to NaCl than *F. sporotrichioides.* The radial expansion of *F. palustre* on NaCl-amended agar plates was unaffected by increasing concentrations up to 0.3 M. *F. sporotrichioides* showed large reductions in growth at the same concentrations. Survival of *M. hapla* was greatest at 0 M, and reduced by half in a 0.3 M solution for 4 days. No juveniles survived exposure to 0.3 M NaCl for 12 days. *M. spartinae* survived at all NaCl concentrations tested, including 1.0 M for at least 12 days. These findings are consistent with the hypothesis that marine organisms in the upper tidal zone must osmoregulate to withstand a wide range of salinity and provide evidence that these pathogens evolved in saline conditions and are not recent introductions from terrestrial niches.

1. Introduction

Most plant pathogens have co-evolved with their ancestral hosts in diverse terrestrial and marine habitats where they have acquired parasitic lifestyles that span from severe pathogens to relatively benign or beneficial endophytes (Papaïx et 2014). The pathogenic fungus, *Fusarium*, and the plant parasitic root-knot nematode, *Meloidogyne* spp., represent two extremely destructive plant pathogen groups. *Fusarium* and *Meloidogyne,* respectively, represent different Kingdoms (Mycota vs. Animalia), and occupy different parasitic lifestyles (facultative vs. obligate), but can work in concert to synergistically increase disease severity (Mai and Abawi, 1987). It has been demonstrated that the interaction between the vascular wilt *Fusarium* species, *F. oxysporum* and the root knot nematode (*Meloidogyne hapla* or *Meloidogyne incognita*) can result in severe disease and complete crop failure in cotton, tobacco, tomato, and watermelon (Mai and Abawi, 1987). Nematodes and fungi have also been shown to cause a decline of European beachgrass, *Ammophila arenaria,* in dune ecosystems (Seliskar and Huettel, 1993; De Rooij-Van der Goes, 1995).

In other natural ecosystems, such as salt marshes, direct losses from pathogens are more difficult to estimate. The value of salt marshes to society, as a whole, is huge in terms of their ability to detoxify contaminants and absorb excess nitrogen and phosphorus, but also as a habitat for marine life and as a buffer for protecting coastal communities from storm surges and wave energy (Bertness, 2007). One estimate (Constanza et al., 1997) adjusted for inflation (Gedan et al., 2009) placed the standing value of salt marsh acreage in 2007 at $14,000/ha.

Spartina alterniflora is the dominant plant in salt marsh environments where salinities can be very high (Hill and Shearin, 1970). Roots of *S. alterniflora* exclude 91–97% of salt ions, depending on salinity, and approximately 50% of the ions absorbed are excreted through shoot salt glands (Bradley and Morris, 1991). As a result of this exclusion, salt concentrations around roots can be higher than

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in other sediments or salt water. Environmental impacts, such as drying, can further increase salt concentrations, while heavy rains can greatly reduce concentrations, particularly at the surface, creating the potential for wide variations in salinity over a matter of hours (Hill and Shearin, 1970).

Recently, a newly described species of *Fusarium*, (*Fusarium palustre*) (Elmer and Marra, 2011) and a re-described species of *Meloidogyne* (*Meloidogyne spartinae*) (Rau and Fassuliotis, 1965; Plantard et al., 2007) were found to be associated with *Spartina alterniflora* in intertidal creek banks affected by Sudden Vegetation Dieback (SVD) (LaMondia and Elmer, 2007; Alber et al., 2008; Elmer and Marra, 2011; Elmer et al., 2013). Studies on the ecology and distribution of these pathogens in intertidal creeks in Connecticut revealed that the low marsh smooth cordgrass, *Spartina alterniflora*, was their only known host (LaMondia and Elmer, 2009; Elmer and Marra, 2011). Greenhouse experiments designed to examine interactions revealed that when both species were inoculated onto *S. alterniflora*, an additive increase in stunting on *S. alterniflora* was observed, but no statistical interaction was detected (Elmer et al., 2011). As there was no mortality, it was concluded they were not causal to SVD, but they may persist in low densities in healthy plants and increase in number when abiotic stresses increase (Elmer and Marra, 2011; Elmer et al., 2011).

One stress that was initially implicated in SVD was increased salinity, although subsequent studies found that drought, and not salinity, was more associated with SVD (Elmer et al., 2013). The *Spartina alterniflora* grass and the pathogens in the intertidal marsh areas along marsh creek banks have greater exposure to a range of salinity than in other areas due to freshwater rainfall and drying of salt water. We had previously determined that *Meloidogyne spartinae* were more numerous in cordgrass roots and developed more quickly in the higher elevations of the intertidal zone (LaMondia and Elmer, 2009). In general, species of *Fusarium* and *Meloidogyne* are not saline-tolerant (Chen, 1964; Edongali et al., 1982), so it became of interest to understand if *Fusarium palustre* and *M. spartinae* had acquired tolerance to salinity and how that tolerance compared to closely related terrestrial species.

With the advent of multiple gene phylogenies to resolve genetic diversity, we can more confidently identify species and determine genetic relatedness. A combined three gene (translation elongation factor-α, beta-tubulin, and calmodulin) sequence topology revealed that *Fusarium palustre's* closest relatives were *Fusarium langsethiae*, a northern European species (Torp and Nirenberg, 2004) and *Fusarium sporotrichioides* a common endophyte on corn and wheat in the US (Vargo and Baumer, 1986) and commonly isolated from corn stubble in Connecticut (Elmer and Ferrandino, 2006). In addition, the 18S rDNA sequence of *Meloidogyne spartinae* was compared to other *Meloidogyne* species (Plantard et al., 2007). Phylogenetic analysis unambiguously identified *Meloidogyne hapla*, a common nematode pathogen of agronomic crops in Connecticut, as the nearest species to *M. spartinae*. Given that both *F. palustre* and *M. spartinae* had closely related local terrestrial species, our aim was to compare each to their near relatives (*F. sporotrichioides* and *M. hapla,* respectively) for tolerance to salinity to determine if these pathogens had acquired tolerance and/preference for saline conditions.

2. Material and methods

2.1. Salt tolerance in Fusarium species

Isolates of *Fusarium palustre* were recovered from *Spartina alterniflora* from several sources in Connecticut and used in the three sets of experiments (Table 1). Details on isolations, culture and identification can be found elsewhere (Elmer and Marra, 2011).

Table 1
Isolates, origin, and habitat of isolates of *Fusarium* spp. used in each experiment.

Fusarium species	Origin and coordinates	Habitat	Expt.[a]
F. palustre			
Ham 06-1 2006	Madison, CT, 41.3333° N, 72.6333° W	Saline marsh	1,2,3
FU2	Westbrook, CT, 41.3000° N, 72.4667° W	Saline marsh	1,2
WRH2	Guilford, CT, 41.2833° N, 72.6833° W	Saline marsh	1,2
Banca 2-2	Branford, CT, 41.2778° N, 72.7997° W	Saline marsh	1,2
WP168 stems site 1	Guilford, CT, 41.2833° N, 72.6833° W	Saline marsh	3
DI E 2	Wells, ME, 43.3203° N, 70.6117° W	Saline marsh	3
WRU1 stems	Guilford, CT, 41.2833° N, 72.6833° W	Corn field	3
PPt H2R	Branford, CT, 41.2778° N, 72.7997° W	Corn field	3
F. sporotrichioides			
U2	North Grosvenordale, CT CT41.985494° N, 71.898719	Corn field	1,2
E4-5	Southbury, CT41.4736° N, 73.2342° W	Corn field	1,2
N2	Thompson, CT41.9844° N, 71.8778° W	Corn field	1,2
A-64	Southbury, CT41.4736° N, 73.2342° W	Corn field	1,2
Y-128-1	North Grosvenordale, CT41.985494° N, 71.898719	Corn field	3
M-128-2	Thompson, CT41.9844° N, 71.8778° W	Corn field	3
E-4-5	Southbury, CT41.4736° N, 73.2342° W	Corn field	3
V-11	North Grosvenordale, CT41.985494° N, 71.898719	Corn field	3
K2	Southbury, CT41.4736° N, 73.2342° W	Corn field	3

[a] Expt. = The experiment was repeated three times. Each experiment had 4–5 isolates replicated three times.

Isolates of *Fusarium sporotrichioides* were recovered from corn stubble in non-saline soils (soluble salts >0.5 mmho/cm) from two areas of the state: Southbury, CT and the northwest corner of Connecticut. Both sites were approximately 30 miles from the coast. Isolates were stored on silica gel at 4 °C (Fisher et al., 1982) and revived on carnation leaf agar as needed (Table 2).

Czapek Dox Agar was prepared with sodium chloride added at the rate of 0, 0.16, 0.31, 0.62, or 0.94 M to mimic 0, 25, 50, 100, or 150% sea water. Petri dishes were prepared and seeded in the middle with a 4-mm agar plug colonized by the test isolate. Plates were grown at 25 °C in the dark. There were three agar plates per isolate per repetition. After 6 days, radial growth measurements were made in two right angle directions from the edge of the plug to advancing tip of the hyphae. The geometric mean was computed from the two determinations per plate. The three replicate dishes per isolate were averaged for each measurement. The percent inhibition of each averaged replicate at each concentration of NaCl was computed by dividing by the radial growth by the radial growth of the same species grown without NaCl and multiplying by 100. The experiment was repeated three times. Isolates within a species served as the replicate and NaCl concentration and species served as main effects. Data were subjected to general linear model and best fits were determined for radial growth after 6 days. All statistics were performed using Systat V.11 (Evanston, IL).

Table 2
Regressions equation parameters for the effect of NaCl concentration on the percent radial growth inhibition of *Fusarium* species.

Species	Curve type[a]	Equation parameters			*F*	*P*	r^2
		Coef, (a)	b (std. Error)	c (std. Error)			
F. sporotrichioides	Linear	98.8	−45.3 (4.1)	–	121.0	>0.001	0.67
	Polynomial 1	79.8	−46.3 (4.7)	−7.3 (15.7)	59.8	>0.001	0.65
	Polynomial 2	92.7	–	−43.6 (4.5)	94.2	>0.001	0.53
F. palustre	Linear	106.2	−27.3 (3.2		72.7	>0.001	0.54
	Polynomial 1	101.3	−19.4 (3.1)	−52.5 (10.0)	66.0	>0.001	0.66
	Polynomial 2	103.6	–	−30.6 (2.8)	118.5	>0.001	0.69

[a] Linear ($Y = a + bx$), Polynomial 1 ($Y = a + bx + cx^2$); Polynomial 2 ($Y = a + cx^2$); where Y = % inhibition and X = NaCl (M).

2.2. Salt tolerance in Meloidogyne species

We conducted experiments to investigate the ability of *Meloidogyne spartinae* from Connecticut to survive a wide range of NaCl concentrations over time. *Meloidogyne hapla* is closely related genetically to *M. spartinae* and a Connecticut population was used in the same experiments for comparison. Juveniles of *M. spartinae* were collected after dissection of naturally infected *Spartina alterniflora* root galls and *M. hapla* juveniles were recovered from egg masses taken from greenhouse-grown *Lobelia* roots placed on pie pans. Juveniles of both species were placed in separate covered counting dishes in 5 ml of 0.0 (distilled water), 0.1, 0.3, 0.5, 0.7, and 1.0 M (roughly 1.6 × sea water) NaCl concentrations and held at ambient laboratory temperature. Nematode viability was determined after 1, 5, and 12 days by observation of motility. Non-motile nematodes were probed with a pick to encourage movement when evaluating survival. There were two replicate dishes of each nematode and the first 10 juveniles observed per dish were counted as motile or not. The experiment was conducted three times. Percent survival was normalized and converted to probits using the NORMSINV (p) function in Excel. Probit data were regressed against salt concentration to linearize data and determine the EC_{50} (NaCl concentration that resulted in 50% mortality) for each nematode-time combination. Because the normsinv transformations of zero and 100 are undefined, zero viability was scored as 0.1% and 100 percent viability was scored as 99.9%. The regression lines were plotted using SigmaPlot (SPSS Inc., Chicago, IL) and the confidence intervals for the parameters were used to determine significant differences.

3. Results

3.1. Salt tolerance in Fusarium species

After 6 days, an inverse linear relationship was evident between NaCl concentration and the percent inhibition of radial growth of *Fusarium sporotrichioides*, but a polynomial relationship was the best fit for *Fusarium palustre* since this species was unaffected by NaCl up to 0.31 M (Fig. 1 Table 2). In fact, *F. palustre* showed no response to increasing levels of NaCl until concentrations increased above 0.31 M, the approximate NaCl concentration found in Connecticut intertidal marshes. At higher concentrations of NaCl, the growth of both species declined in the same fashion and the slopes of the curves did not statistically indicating they differed only in the threshold where the NaCl became inhibitory.

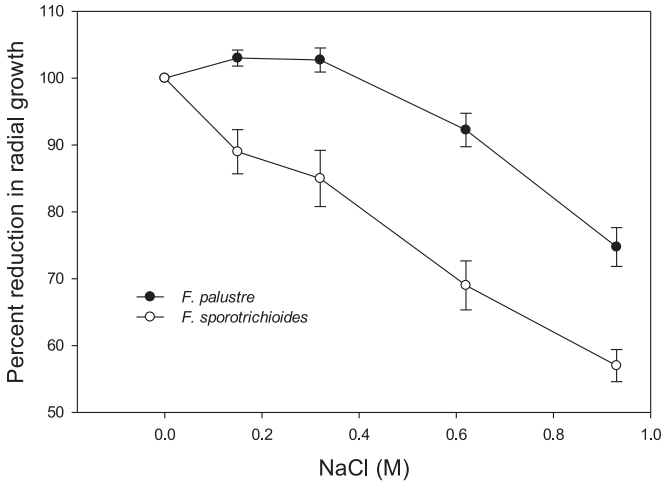

Fig. 1. Effect of NaCl (M) concentrations on the percent inhibition of radial growth of *Fusarium palustre* and *F. sporotrichioides* after 6 days on agar containing increasing concentration of NaCl. Error bars represent the standard error of the means averaged over three repetitions.

3.2. Salt tolerance in Meloidogyne species

In each of the three repetitions of the experiment, *Meloidogyne hapla* survived best in distilled water and did not survive 12 days exposure to 0.3 M NaCl (Fig. 2). Maximum survival of *M. hapla* was 100% of juveniles examined in the distilled water control at 6 days and in 0.1 M NaCl at 2 days. Survival of *M. hapla* was reduced by half by exposure to a 0.3 M solution for 4 days. *Meloidogyne spartinae*, on the other hand, survived at all concentrations tested for at least 12 days; maximum survival was 83.5% of juveniles examined, and survival was approximately 60% or greater in salinity ranging from distilled water to 0.5 M NaCl for all times tested, and up to five days at 0.7 M or one day at 1.0 M. A low level of survival was observed after 12 days at 1 M. The confidence intervals (2 × standard error) did not overlap for the regression coefficients for days of exposure, salt concentration or intercept, so the models for the two nematodes were significantly different. The Normsdist function in Excel can be used to convert the normsinv variable to percent viability.

4. Discussion

Spartina alterniflora can withstand high salinities (Hill and Shearin, 1970) so it is not surprising to see associated microbes exhibiting tolerance to NaCl. *Fusarium palustre* stands as a NaCl-tolerant species when compared to *Fusarium sporotrichioides*. There was no inhibition in radial growth of *F. palustre* as NaCl concentrations approached 0.31 M NaCl/liter. In fact, many isolates of *F. palustre* showed slightly faster growth as NaCl concentrations increased to the level associated with marsh water (0.27–0.32 M NaCl).

In general, *Fusarium* spp. are not halotolerant, which is defined as being able to grow at concentration above 1.7 M NaCl (100 g NaCl/liter) (Gunde-Cimerman et al., 2009), but many species can persist in saline soils. In a study conducted in arid saline terrestrial soils, Mandeel (2006) reported that *Fusarium solani* was the most saline-tolerant species recovered from soil dilutions on 5% NaCl amended agar.

Meloidogyne spartinae is widely distributed from New England to the Gulf coast, however, *Spartina alterniflora* populations from northern areas generally had more numerous and larger galls than those from southern areas, suggesting that northern collections

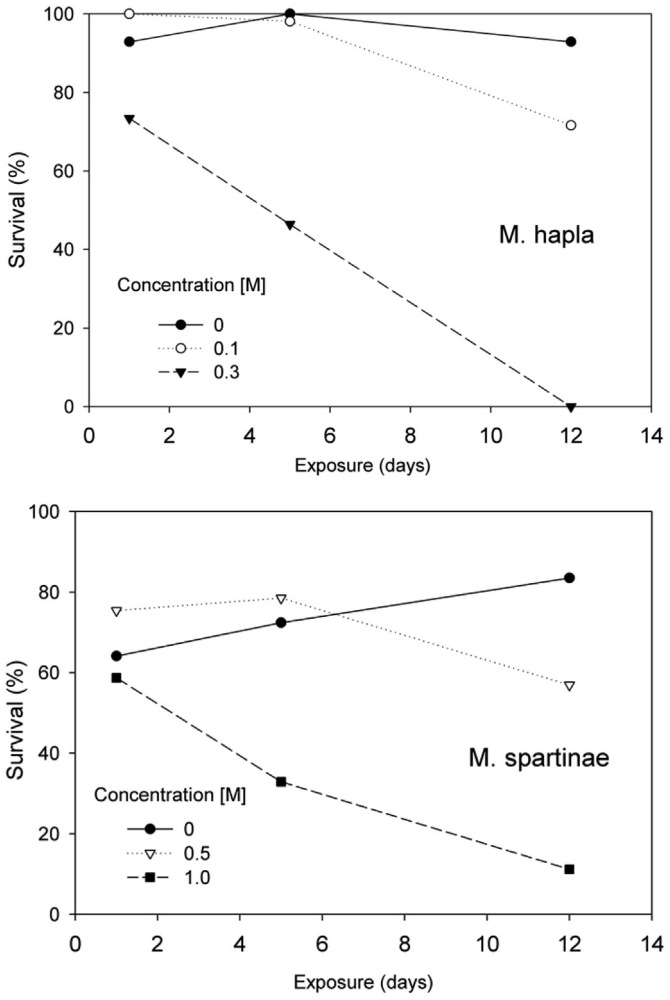

Fig. 2. The effects of sodium chloride concentration on survival of *Meloidogyne hapla* and *M. spartinae* over time. The model for *M. hapla* was: Normsinv Viability = −9.765 (concentration) −0.172 (days) + 3.614; $R^2 = 0.85$, $P = \leq 0.0001$. The model developed for *M. spartinae* was: Normsinv Viability = −1.579 (concentration) −0.0.064 (days) + 1.48; $R^2 = 0.34$, $P = \leq 0.0001$.

were more susceptible to the nematode (Seneca, 1974). Egg hatch and development were greater for *M. spartinae* in 0.2–0.4 M salt solutions compared to 0.0, 0.1, or 1.0 M (Fassuliotis and Rau, 1966). In contrast, hatching of *Heterodera rostochiensis* and *Meloidogyne arenaria* cyst and root-knot nematodes was inhibited in solutions between 0.2 and 0.4 M NaCl (Dropkin et al., 1958). Other root-knot species, such as *Meloidogyne incognita* and *Meloidogyne javanica,* have been shown to be repelled by salts, with movement occurring from higher to lower concentrations (Prot, 1978, 1979). Infectivity and development was also shown to be impaired after exposure to salt (Edongali et al., 1982). In fact, Castro et al. (1991) suggested that creating salt gradients using fertilizers might be utilized as a management tactic for nematode exclusion.

Our results with *Meloidogyne hapla* were similar to these other root-knot species in that survival was poor at NaCl levels above 0.1 M. Survival of *M. hapla* was reduced by half by exposure to a 0.3 M solution for 4 days. In contrast, *Meloidogyne spartinae* survival was greatest at 0.0–0.5 M (the levels commonly associated with marsh water and soils) and survival was reduced by half after 4 days only by exposure to a 1.0 M solution. This range of salt tolerance indicates that *M. spartinae* can survive and move in marsh sediments at salt concentrations ranging from fresh rain water to those 1.6 × higher than sea water.

The pathogens *Fusarium palustre* and *Meloidogyne spartinae* were associated with *Spartina alterniflora* in marsh locations affected by SVD (LaMondia and Elmer, 2007; Elmer and Marra, 2011; Elmer et al., 2013). No other plant parasitic nematodes were found infecting *S. alterniflora* in sampled marshes. To date, both of these pathogens have only been described infecting *S. alterniflora*. It would be reasonable to assume that salt tolerance imparts a selective advantage to both *F. palustre* and *M. spartinae* and may explain the dominance of these pathogens in salt marsh ecosystems (Elmer et al., 2013). The closest related nematode to *M. spartinae*, *Meloidogyne hapla*, would not survive in typical *S. alterniflora*-dominated marshes.

Bryne and Jones (1975) reported that, in general, terrestrial ascomycetes showed limited tolerance to high salinity whereas marine ascomycetes tend to have a wide tolerance of salinity conditions. These findings are consistent with ours and support the hypothesis that marine organisms in the upper tidal zone that are exposed to extremes in salinity must be able to osmoregulate to withstand a wide range of salinity. In addition, these data provide evidence that these pathogens may have evolved in saline conditions and are not recent introductions from terrestrial niches.

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References

Alber, M., Swenson, E.M., Adamowicz, S.C., Mendelssohn, I.A., 2008. Salt marsh dieback, an overview of recent events in the US. Estuar. Coast. Shelf Sci. 80, 1–11.
Bertness, M.D., 2007. Atlantic Shorelines. Princeton University Press, Princeton, NJ.
Bradley, P.M., Morris, J.T., 1991. Relative importance of ion exclusion, secretion and accumulation in *Spartina alterniflora* Loisel. J. Exp. Bot. 42, 1525–1532.
Bryne, P.J., Gareth Jones, E.B., 1975. Effect of salinity on the reproduction of terrestrial and marine fungi. Trans. Br. Mycol. Soc. 65, 185–200. http://dx.doi.org/10.1016/S0007-1536(75)80002-7.
Castro, C.E., McKinney, H.E., Lux, S., 1991. Plant protection with inorganic ions. J. Nematol. 23, 409–413.
Chen, A.W., 1964. Soil fungi with high salt tolerance. Trans. Knaswa Acad. Sci. 67, 36–40.
Costanza, R., D'Arge, R., DeGroot, R., Farber, S., Grasso, M., 1997. The value of the world's ecosystem services and natural capital. Nature 387, 253–280.
De Rooij-Van der Goes, P.C.E.M., 1995. The role of plant-parasitic nematodes and soil-borne fungi in the decline of *Ammophila arenaria* (L.) Link. New. Phytol. 129, 661–669.
Dropkin, V.H., Martin, G.C., Johnson, R.W., 1958. Effect of osmotic concentration on hatching of some plant parasitic nematodes. Nematologica 3, 115–126.
Edongali, E.A., Duncan, L., Ferris, H., 1982. Influence of salt concentration on infectivity and development of *Meloidogyne incognita* on tomato. Rev. Nematol. 5, 111–117.
Elmer, W.H., Ferrandino, F.J., 2006. Distribution of *Fusarium* species on corn stubble in Connecticut. Phytopathology 96, S32 (abstr.).
Elmer, W.H., LaMondia, J.A., Caruso, F., 2011. Association between *Fusarium* spp. on *Spartina alterniflora* and dieback sites in Connecticut and Massachusetts. Estuar. Coasts 35, 436–444. http://dx.doi.org/10.1007/s12237-011-9448-9.
Elmer, W.H., Marra, R.E., 2011. New species of *Fusarium* associated with dieback of *Spartina alterniflora* in Atlantic salt marshes. Mycologia 103, 806–819.
Elmer, W.H., Useman, S., Schneider, R.W., Marra, R.E., LaMondia, J.A., del Mar Jimenez-Gasco, M., Mendelssohn, I.A., Caruso, F.L., 2013. Sudden vegetation dieback in Atlantic and gulf coast salt marshes. Plant Dis. 97, 436–445.
Fassuliotis, G., Rau, G.J., 1966. Observations on the embryogeny and histopathology of *Hypsoperine spartinae* on smooth cordgrass roots, *Spartina alterniflora*. Nematologica 13, 90.
Fisher, N.L., Burgess, L.W., Toussoun, T.A., Nelson, P.E., 1982. Carnation leaves as a substrate and for preserving cultures of *Fusarium* species. Phytopathology 72, 151–153.
Gedan, K.B., Silliman, B.R., Bertness, M.D., 2009. Centuries of human-driven change in salt marsh ecosystems. Annu. Rev. Mar. Sci. 1, 117–141.
Gunde-Cimerman, N., Ramos, J., Plemenitas, A., 2009. Halotolerant and halophilic fungi. Mycol. Res. 113, 1231–1241.

Hill, D.E., Shearin, A.E., 1970. Tidal Marshes of Connecticut and Rhode Island. Bulletin 709. The Connecticut Agricultural Experiment Station.
LaMondia, J.A., Elmer, W.H., 2007. Occurrence of *Meloidogyne spartinae* on *Spartina alterniflora* in Connecticut and Massachusetts. Plant Dis. 91, 327.
LaMondia, J.A., Elmer, W.H., 2009. Ecological relationships between *Meloidogyne spartinae* and salt marsh grasses in Connecticut. J. Nematol. 40, 217–220.
Mai, W.F., Abawi, G.S., 1987. Interactions among root-knot nematodes and *Fusarium* wilt fungi on host plants. Annu. Rev. Phytopathol. 25, 317–338.
Mandeel, Q.A., 2006. Biodiversity of the genus *Fusarium* in saline soil habitats. J. Basic. Microbiol. 46, 480–494.
Papaïx, P., Burdon, J.J., Lannou, C., Thrall, P.H., 2014. Evolution of pathogen specialisation in a host metapopulation, joint effects of host and pathogen dispersal. PLoS One 10, 1371. http://dx.doi.org/10.1371/journal.pcbi.103633.
Plantard, O., Valette, S., Gros, M.F., 2007. The root-knot nematode producing galls on *Spartina alterniflora* belongs to the genus *Meloidogyne*, rejection of *Hypsoperine* and *Spartonema* spp. J. Nematol. 39, 127–132.
Prot, J.-C., 1978. Influence of concentration gradients of salts on the movement of 2nd stage juveniles of *Meloidogyne javanica*. Rev. Nematol. 1, 21–26.
Prot, J.-C., 1979. Influence of concentration gradients of salts on the behavior of four plant parasitic nematodes. Rev. Nematol. 2, 11–16.
Rau, G.J., Fassuliotis, G., 1965. *Hypsoperine spartinae* n. sp., a gall-forming nematode on the roots of smooth cordgrass. Proc. Helminthol. Soc. Wash. 32, 159–162.
Seliskar, D.M., Huettel, R.N., 1993. Nematode involvement in the dieout of *Ammophila breviligulata* (Poaceae) on the mid-Atlantic coastal dunes of the United States. J. Coast. Res. 9, 97–103.
Seneca, E.D., 1974. Germination and seedling response of Atlantic and Gulf coast populations of *Spartina alterniflora*. Am. J. Bot. 61, 947–956.
Torp, M., Nirenberg, H.I., 2004. *Fusarium langsethiae* sp. *nov.* on cereals in Europe. Int. J. Food Microbiol. ISSN: 0168-1605 95, 247–256. http//dx.doi.org/10.1016/j.ijfoodmicro.2003.12.014.
Vargo, R.H., Baumer, J.S., 1986. *Fusarium sporotrichioides* as a pathogen on spring wheat. Plant Dis. 70, 629–631.