Mycorrhiza (2003) 13:177–183
DOI 10.1007/s00572-003-0232-y

REVIEW

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Compatible host/mycorrhizal fungus combinations for micropropagated sea oats

I. Field sampling and greenhouse evaluations

Received: 26 March 2002 / Accepted: 11 February 2003 / Published online: 4 April 2003

Abstract Micropropagation technology promises to improve the supply of sea oats for restoring Florida's eroded beaches, but concerns about genetic diversity need to be addressed. These dune plants are colonized by a wide array of arbuscular mycorrhizal (AM) fungi, yet little is know of the diversity of these fungal communities. Our goal was to test the level of functional diversity that exists among communities of AM fungi that are present in divergent Florida dunes. Community pot cultures were established from samples collected from ten transects in two Gulf coast and two Atlantic coast locations in Florida, and these were used to conduct two greenhouse studies. The objective of the first study was to evaluate within-location variance in the mycorrhizal function of different AM fungal communities associated with endemic sea oats. The objective of the second study was to evaluate among-location responses of plant and fungal ecotypes using selected combinations obtained from the first experiment. Within locations, the AM fungal community had significant impacts on shoot mass and shoot-P contents, confirming a range of symbiotic effectiveness exists within the beach-dune system. Among locations, there was a tendency for greater root colonization between host clones and fungal communities from the same location, indicating a degree of specificity between host ecotypes and their symbiotic fungi. Relative to plant growth response, one fungal community was superior across plant genotypes from all locations, while one plant genotype tended to have the best response across all fungal communities. These data suggest that while it is possible to select effective AM fungal-host combinations for outplanting, origin of host and AM fungi have little predictive value in screening these combinations.

Keywords Dune ecology · Ecotype · Effectiveness · Florida · Functional diversity

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Introduction

More than 50% of Florida's 1,300 km of sandy beaches are experiencing erosion, with approximately 500 km in a critical state of erosion (Anonymous 1999). Beach nourishment — where sand is collected from an offshore location and piped onto the beach — followed by planting of appropriate dune plants is the method of choice for restoring Florida beaches (Dean 1983). Revegetation is critical to the process because dune plants provide a defense against the erosive forces of wind and waves (Woodhouse 1982). In the southeastern United States, sea oats (*Uniola paniculata* L.) are the dominant plant growing in the pioneer zone of coastal dunes (Woodhouse et al. 1968). To revegetate Florida's eroded beaches with a recommended 6- to 9-m-wide planting area, 24–36 million sea oats would be required. Techniques that insure reliable plant stands, improve quality, and decrease establishment time would contribute greatly to reducing the cost of beach restoration.

Nursery-grown sea oats, initiated from field-collected seed, are the major plant material currently available for revegetating beaches. Declining natural stands, however, have led to restrictions in field harvesting of sea oats. Micropropagation technology is being developed to improve the supply of plant materials for outplanting (Philman and Kane 1994) although, genetic diversity is a critical issue for field implementation of this technology. Recently, Ranamukaarachchi et al. (personal communi-

cation) used arbitrarily selected random primers to demonstrate significant ecotypic variation among divergent populations of sea oats.

Arbuscular mycorrhizal (AM) fungi are abundant and diverse in natural dune systems and have an important role in maintaining ecosystem stability on nourished beaches (Sylvia 1989; Sylvia and Will 1988). The composition and diversity of AM fungal communities can have a large impact on plant biodiversity and ecosystem productivity (van der Heijden et al. 1998). This is because various AM fungi colonize plant roots to different degrees (termed "infectiveness") and have variable effects on plant growth and development (termed "effectiveness"). These properties may be under the genetic control of the host, the fungus, or more likely a complex interaction of both symbiotic partners with soil environmental factors.

On the host side, Johnson et al. (1991) found that cropping history altered the communities of AM fungi in soil, Bever et al. (1996) demonstrated host-dependent sporulation among common lawn plants, and Zhao et al. (1997) reported differential development of AM fungi with two legume species. Host genotype variation in infectiveness and effectiveness has been demonstrated for a number of plants, including citrus (Graham and Eissenstat 1994), pea (Mårtensson and Rydberg 1995), wheat (Hetrick et al. 1996), barley (Baon et al. 1993), and tomato (Barker et al. 1998). The availability of well-characterized sea oats' ecotypes (Ranamukhaarachchi et al., personal communication) provided an excellent opportunity to investigate host effects on the mycorrhizal symbiosis in the beach-dune system.

Less is known about the effect of fungal genetics on root colonization and plant response. However, variation among AM fungi has been reported (Boyetchko and Tewari 1995; Monzon and Azcon 1996), supporting the hypothesis that fungal ecotype will have an important impact on the symbiotic interaction. For maintaining stability of the beach-dune ecosystem, knowledge of the biodiversity of the fungal partner may be just as important as the biodiversity that occurs in the host plant.

Biodiversity may be viewed as comprising three elements: taxonomic, genetic, and functional (Solbrig 1991). Much mycorrhizal research has focused on taxonomic diversity and, with the advent of the new molecular tools, increasing emphasis is being placed on genetic diversity. However, fewer studies focus on the manner by which genetic or taxonomic diversity affects ecosystem function. Boucher et al. (1999) reported that different mycorrhizal fungi had varying effects on the physiology of maize, while Stahl et al. (1990) demonstrated that different isolates of the same mycorrhizal species had different effects on plant growth. We previously observed a diverse community of mycorrhizal fungi associated with sea oats in Florida dunes (Sylvia 1986). The next step was to better understand the functional significance of this diverse community of fungi on the establishment and growth of dune plants.

The goal of our research was to test the level of functional diversity existing among communities of AM fungi present in divergent Florida dunes. Community pot cultures were established from four locations along Florida's coast and used to conduct two greenhouse studies. The objective of the first study was to evaluate within-location variance in the mycorrhizal function of different AM fungal communities associated with endemic sea oats. The objective of the second study was to evaluate among-location responses of plant and fungal ecotypes using selected combinations obtained from the first experiment.

Materials and methods

Field sampling

Rhizospheres of sea oats were sampled between 22 June and 2 July 2000 from four locations in Florida, two from the Atlantic coast and two from the Gulf coast. The Atlantic coast locations were in northeast Florida [Anastasia State Recreation Area (AN), 29°53′15″N/081°17′23″W] and east-central Florida [Sebastian Inlet State Recreation Area (SI), 27°46′42″N/080°29′27″W]. The Gulf coast locations were in northwestern Florida [St. George Island State Park (SG), 29°39′20″N/084°52′53″W] and west-central Florida [Egmont Key National Wildlife Refuge (EK), 27°35′15″N/082°45′45″W]. The pH and water-extractable P concentrations, respectively, at each location were: AN, 8.3 and 25.9 μg ml^{-1}; SI, 8.5 and 14.5 μg ml^{-1}; SG, 7.6 and 5.0 μg ml^{-1}; EK, 8.4 and 10.7 μg ml^{-1}.

At each location, ten sampling transects were located at a distance of approximately 40 m apart along the primary dune. Transects were established in areas where sea oats replanting had not occurred, as well as could be determined from agency records. Three samples were collected along each transect in the root zone of clumps of pure sea oats. One-liter samples were collected at depths of 20–40 cm, sealed in plastic bags, and placed in an ice chest for transport back to the laboratory. In addition, root-free sand was collected in front of the dune for use in pot culturing. Upon return to the laboratory, spores of AM fungi were sieved from a 200-g subsample from well-mixed composites of the three samples collected along each transect, and root colonization was assessed using the gridline-intersect method (Sylvia 1994).

Community pot cultures of AM fungi were established from the composite of each transect. Root-free sand from each location was mixed 1:1 with coarse vermiculite, moistened, and pasteurized at 85°C for 8 h with dry heat. These substrates were placed into 1.5-l pots and mixed with 500 g (dry mass basis) of corresponding soil collected from each transect. Micropropagated sea oats from each location (clones AN 16–1-7, SI 3–1-3, SG 20–2-2, and EK 16–3-2) were placed in pots with the corresponding substrate and transferred to the greenhouse on 14 July 2000. A dilute (0.1× concentration for all nutrients except P which was at 0.01× concentration) Hoagland's solution (Hoagland and Arnon 1938) was applied to the pots on a weekly basis and plants were watered with deionized water as needed.

Greenhouse studies

The goal of experiment one was to select effective AM fungal community-host genotype combinations from each of the four locations (within location effects). Community cultures of AM fungi from three randomly selected transects from each location were used to inoculate three genotypes of sea oats that were obtained from the same location and maintained in tissue culture (Philman and Kane 1994). The substrate consisted of root-free sand

from each location mixed 1:1 with coarse vermiculite as above. These substrates were placed into 1.5-l pots and 20 g of the appropriate inoculum was place in a band below the soil surface. Micropropagated sea oats were placed in pots with corresponding substrate and fertilized with the dilute Hoagland's solution as above.

The experiment had three AM fungal community treatments, three host treatments, and six replicates per treatment combination resulting in a total of 54 experimental units for each location. A standardized mycorrhizal infection potential (MIP) assay (Sylvia 1994) was conducted on each inoculum when the experiment was initiated using *Zea mays* L. as the host. Inoculated plants were grown in the greenhouse from 8 March 2001 until 8 May 2001. Average maximum and minimum greenhouse temperatures during the experiment were 32°C and 18°C, respectively, and the average maximum photosynthetic photon flux density (PPFD) was 1,235 μmol m^{-2} s^{-1}. At harvest, shoot and root dry masses were determined. Total and AM fungal colonized root lengths were estimated by the gridline-intersect method. Shoots were ground to pass a 20-mesh sieve, ashed, and analyzed for P content using the method of Murphy and Riley (1962). A general linear model (SAS Institute 1989) was applied to the data to test for the main effects and their interactions on all response variables at each location.

The goal of experiment two was to evaluate AM fungal community-host ecotype compatibility of AM fungi and sea oats collected from the four dune locations (among location effects). AM fungal-host combinations that produced superior shoot dry mass in experiment one were tested in a factorial combination using four AM fungal communities and four host ecotypes (i.e., one from each location) with six replicates per treatment combination for a total of 96 experimental units. Pot size, substrates, inoculation methods, and fertilizer regime were the same as for experiment one.

A standard MIP assay was conducted on each inoculum when the experiment was initiated. Inoculated plants were grown in the greenhouse from 8 June 2001 until 8 September 2001. Average maximum and minimum greenhouse temperatures during the experiment were 35°C and 23°C, respectively, and the average maximum PPFD was 1,230 μmol m^{-2} s^{-1}. At harvest, shoot and root biomass, shoot-P content, and extent of root length colonized by AM fungi were evaluated. A general linear model was applied to the data to test for the main effects and their interactions on all response variables.

Results and discussion

Field sampling

Sea oats were colonized by AM fungi in the natural dune systems (Table 1), although percentage colonization was lower than previously reported (Sylvia 1986). Communities of AM fungi included six to 19 species at each location, including seven of *Glomus*, six of *Acaulospora*, four of *Scutellospora*, and four of *Gigaspora*. Spore densities were higher in Gulf coast samples (SG and EK), but this was largely due to the presence of spores clusters of *Glomus microaggregatum* that frequently sporulated inside dead spores and other organic debris (Koske et al. 1986).

Experiment one (within location)

ANOVA revealed that the transect-specific AM fungal communities often had a highly significant ($P \leq 0.01$) effect on measured variables (Table 2). The only exceptions were root dry mass in sand from Anastasia, and shoot dry mass, root dry mass, and shoot-P content in sand from St. George. Host genotype had fewer effects on measured variables, with significance mostly occurring with root dry mass production. Interactions among host genotype and AM fungal community occurred only in the Anastasia sand for shoot and dry mass, and shoot-P content, and in Sebastian sand for colonized root length.

Some fungal communities from the Atlantic coast (AN and SI) colonized their hosts more aggressively than others (Fig. 1A–D); however, these aggressive colonizers did not necessarily produce the greatest plant root mass (Fig. 1E–H), shoot mass (Fig. 1I–L), or shoot-P content (Fig. 1M–P). The AM fungal community had significant impacts on shoot mass and shoot-P contents in all locations but SG; however, in SG substrate root mass was affected. These data confirm that a range of symbiotic infectiveness and effectiveness exists within the beach-dune system (Sylvia and Burks 1988), and afforded the opportunity for selection of compatible AM fungal-host combinations from each location.

Experiment two (among locations)

There were highly significant effects of both host ecotype and selected fungal community on all measured variables, except root dry mass for the AM treatment (Table 3). There were no significant host ecotype×AM fungal community interactions for shoot and root dry mass and shoot-P content; however, there was a significant interaction for root colonization.

Table 1 Arbuscular mycorrhizal (AM) fungal root colonization, species richness, and spore density in samples collected from rhizospheres of sea oats (*Uniola paniculata* L.) in four Florida locations

Location	Root colonization (%)[a]	Species richness	Total spore density (per 200 g)[a]
Atlantic coast			
Anastasia	24±6	6	20±8
Sebastian	12±4	12	12±3
Gulf coast			
St. George	10±1	19	202±58[b]
Egmont	34±7	12	1,004±168[c]

[a] Values are means of ten replicates±SEM
[b] 32% of spores were *Glomus microaggregatum*
[c] 69% of spores were *G. microaggregatum*

Table 2 *P*-values from ANOVA for experiment one evaluating sea oats' genotype (*Host*) and AM fungal community (*AM*) within-location responses from four Florida beach locations

Treatments	Shoot dry mass	Root dry mass	Colonized root length	Shoot-P content
Anastasia — Atlantic coast				
Host	0.3449	0.0092	0.0006	0.4709
AM	0.0002	0.1987	0.0001	0.0010
Host×AM	0.0002	0.0120	0.1670	0.0005
Sebastian — Atlantic coast				
Host	0.1108	0.2534	0.1202	0.0481
AM	0.0003	0.0001	0.0001	0.0008
Host×AM	0.9582	0.9860	0.0001	0.9626
St. George — Gulf coast				
Host	0.7591	0.0048	0.1608	0.5882
AM	0.2785	0.0144	0.1062	0.1986
Host×AM	0.9699	0.6681	0.4856	0.9638
Egmont — Gulf coast				
Host	0.4345	0.0004	0.8280	0.3825
AM	0.0001	0.0051	0.0001	0.0008
Host×AM	0.1556	0.6353	0.2977	0.0855

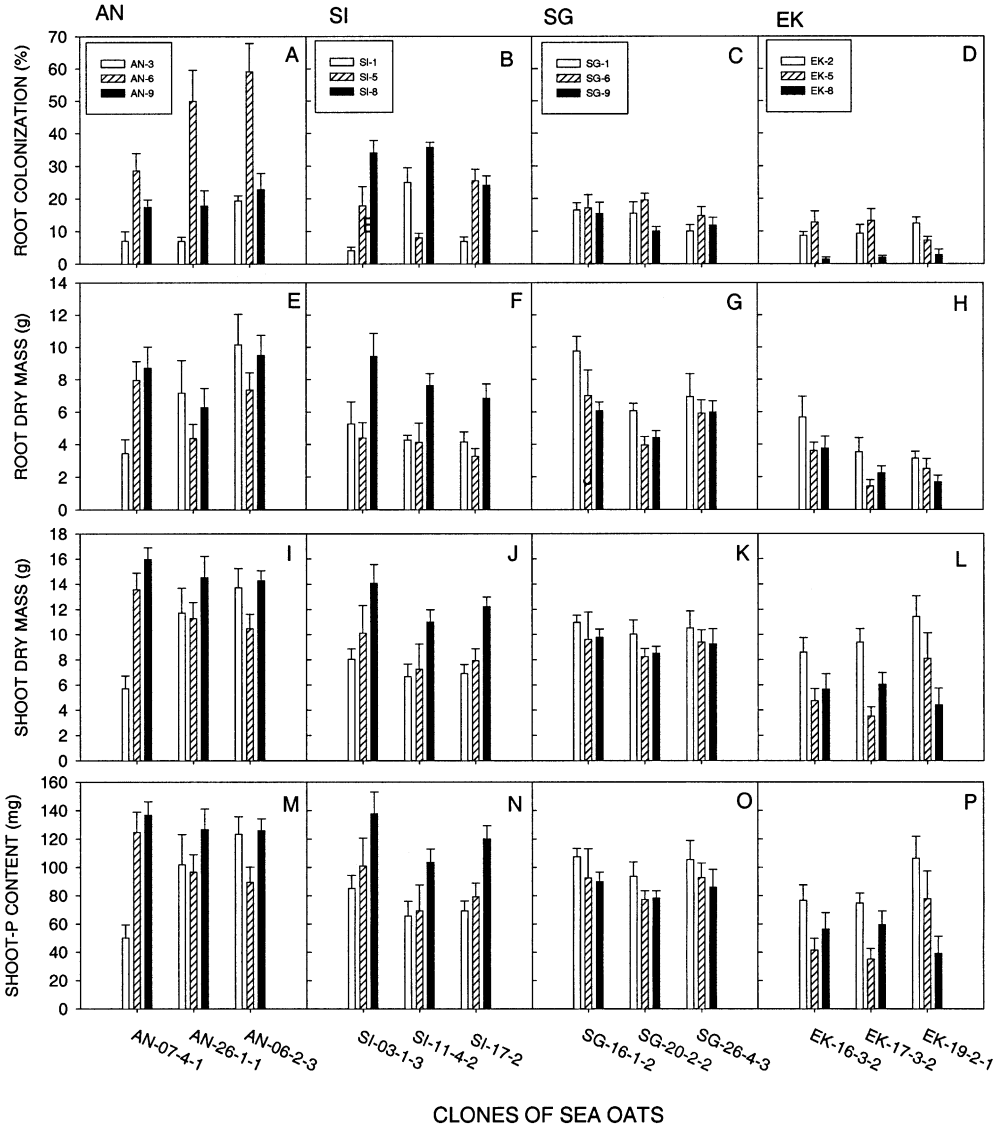

Fig. 1 Effect of host genotype and AM fungal community on root colonization (**A–D**), root dry mass (**E–H**), shoot dry mass (**I–L**), and shoot-P content (**M–P**) of sea oats from four beach locations in Florida [Anastasia State Recreation Area (*AN*), Sebastian Inlet State Recreation Area (*SI*), St. George Island State Park (*SG*), and Egmont Key National Wildlife Refuge (EK)]. *Box labels* designate AM fungal communities. *Bars* represent the mean of six replicates±SEM

Table 3 *P*-values from ANOVA for experiment two evaluating sea oats' ecotype (*Host*) and selected AM fungal community (*AM*) among-location responses of four Florida beach locations

Treatments	Shoot dry mass	Root dry mass	Colonized root length	Shoot-P content
Host	0.0008	0.0097	0.0081	0.0001
AM	0.0001	0.1726	0.0080	0.0001
Host×AM	0.8190	0.9414	0.0006	0.8627

There was a tendency for greater root colonization between host ecotypes and fungal communities from the same location; e.g., clone AN-07–4-1 with fungal community AN-9 and clone SG-16–1-2 with fungal community SG-1 (Fig. 2A). Some host ecotypes were poorly colonized by fungal communities that came from different locations; e.g. SG-16–1-2 and EK-17–3-2 with AN-9. The AM fungi have the ability to colonize a vast taxonomic range of plants, indicating a general lack of host specificity (Gianinazzi-Pearson 1984). Our data, however, indicate some specificity between host ecotypes and their symbiotic fungi and support other studies indicating "host preference" in plant-fungal associations. For example, Zhu et al. (2000) reported quantitative host preference by perennial ryegrass (*Lolium*) and white clover (*Trifolium*) for AM fungi associated with their own rhizospheres.

Relative to plant growth response, one fungal community (SG-1) was superior across plant clones from all locations (Fig. 2B–D). Furthermore, one plant clone (EK-17–3-2) tended to have the best growth response across all fungal communities. It is well known that infectivity and effectiveness are not necessarily positively correlated (Gianinazzi-Pearson et al. 1985). Interestingly, Feldmann (1998) recently demonstrated that within three subsequent inoculation cycles using inocula derived from a single spore, a range of effectiveness from negative through positive may develop. In addition to infectivity, innate differences in P-inflow rates (Al-Nahidh and Sanders 1987) and tolerance of environmental stresses (Enkhtuya et al. 2000) may contribute to variable effectiveness among AM fungi.

Inoculum density may be a confounding factor when comparing the effectiveness of various AM fungi (Clapperton and Reid 1992). Therefore, an assessment of inoculum density is important for interpreting the outcome of inoculation trials. In our study we used the MIP assay for this purpose. In experiment one we calculated a mean MIP of 54% root length colonization (range 41–71%) for the 12 inocula, and in experiment two we calculated a mean colonization of 45% (range 44–50%). The fairly narrow range of MIP values, especially in experiment two, indicate that widely differing inoculum densities were not confounding our experimental results and, furthermore, no correlation was found between MIP estimates and measured variables (data not presented).

The degree of adaptation of AM fungi to their environment is still largely an open question. Henkel et al. (1989) found that differences in infectiveness and effectiveness occurred among AM fungi from parent soils that were dissimilar yet contiguous, indicating a degree of

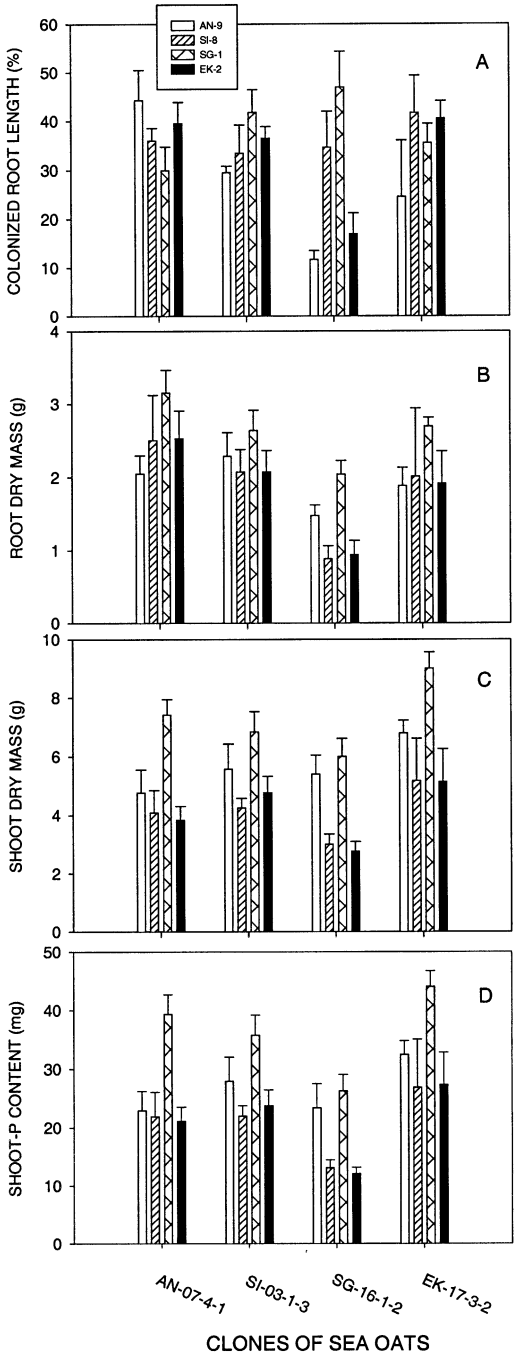

Fig. 2 Effect of host ecotype and AM fungal community on root colonization (**A**), root dry mass (**B**), shoot dry mass (**C**), and shoot-P content (**D**) of sea oats. *Box labels* designate AM fungal communities. *Bars* represent the mean of six replicates±SEM

adaptation of the native fungi to their soil environment. Schultz et al. (2001) found that *Andropogon* from two locations with differing fertility grew better in its own soil indicating adaptation to fungi from their soil of origin. Ronsheim and Anderson (2001) reported specificity in the interaction between *Allium* plants and the soil fungal community that favored intraspecific interactions among plants. In our system, we observed that the soil of origin was important relative to infectiveness, but not effectiveness.

Our greenhouse studies suggest that it is possible to select AM fungal-host combinations that produce greater plant growth for outplanting; however, origin of host and AM fungi may have little predictive value in screening for compatible combinations. Further studies should be conducted to evaluate the life strategies of specific fungi within the communities in order to improve our ability to predict growth response in situ (Hart et al. 2001). Future research should evaluate these responses in the field and test variations among single-species cultures within and among locations.

Acknowledgements Published as Florida Agricultural Experimental Station Journal Series no. R-08911. Partial support for this project was obtained from the Office of Sea Grant, National Oceanic and Atmospheric Administration, U.S. Department of Commerce (grant no. NA76RG0120). We thank James Graham and Peter Stahl for reviewing this manuscript.

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