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Population variation of invasive *Spartina alterniflora* can differentiate bacterial diversity in its rhizosphere

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Abstract While several studies have documented that invasive plants can change the microbial communities, little is known about how soil microbial communities respond to population variation of invasive plants. Here, nine populations of *Spartina alterniflora* were selected from the east coast of China along latitudinal gradient to compare bacterial diversity of rhizospheres among these populations. The bacterial diversity in *S. alterniflora* rhizospheres was valued by denaturing gradient gel electrophoresis (DGGE) analysis. Shannon–Weaver diversity index (H') and number of DGGE bands showed that rhizosphere bacterial diversity of *S. alterniflora* populations increased along a latitudinal gradient when all the populations were grown in a common garden. These findings suggest that population variation of *S. alterniflora* can differentiate the rhizosphere bacterial diversity, and the latitudinal gradient can shape the specific plant–bacterial diversity relationship. Our results adding to the recent literature suggest that invasive plant–soil biota interactions would have clinal variation with environmental gradients and improve our understanding of the mechanisms and processes of plant invasions.

Keywords Bacterial diversity · Plant invasion · Plant–soil feedbacks · Population variation · *Spartina alterniflora*

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Introduction

Soil microbial communities and their ecosystem functions can be altered by invasive plants. For example, two invasive species, *Berberis thunbergii* and *Microstegium vimineum*, have been demonstrated to alter soil microbial composition and structure, microbial enzyme activities, and respiration (Kourtev et al. 2002). While several studies have documented the community responses of microbes to plant invasions (e.g., Batten et al. 2006; Nie et al. 2009), less is known about how soil microbial communities respond to population variation of invasive plants (Batten et al. 2006; Ehrenfeld 2003; Wang et al. 2007).

Recent studies have suggested that population differentiation of invasive plants is an important strategy that allows alien plants to invade new areas successfully (Bossdorf et al. 2005; Sakai et al. 2001). Under new environments of the invaded ecosystems, invasive plants have different morphological and physiological characteristics and new interactions with native plants and organisms of other trophic levels (Burns 2006; Franks et al. 2008; Funk 2008; Xu et al. 2007; Zou et al. 2008). Microbial communities are regulated by the quantity and quality of root exudates into soil, which are, in turn, affected by species–environment interactions (Broughton and Gross 2000; Chapman et al. 2003; Ehrenfeld 2004; Grayston et al. 1998). Variation in the plant traits and subsequent changes in litter and root exudation in different environments can lead to the shift in microbial community structure (Broughton and Gross 2000; Jones et al. 2004; Paterson et al. 2007). These studies suggest that the population variation of invasive plants may have different impacts on their rhizosphere microbial communities.

In order to investigate the relationship between population variation of invasive plants and soil microbial communities, nine populations of *S. alterniflora* were collected from the east coast of China along latitudinal gradient to compare bacterial diversity of rhizospheres among those populations. *S. alterniflora* native to North America is invasive to salt marshes worldwide (Craft et al. 1999; Wang et al. 2006). The geographic distribution of *S. alterniflora* in China has been expanding to most of the east coast since it was first introduced in 1979 (An et al. 2007). Many studies have shown that *S. alterniflora* has different growth characteristics, phenology, and genome size, depending on geographic regions (Anderson and Treshow 1980; Freshwater 1988; Seneca 1974). Rapid population differentiation in response to the wide range of environments contributes to successful invasion of this plant species in salt marshes (Blum et al. 2007; O'Brien and Freshwater 1999; Perkins et al. 2002; Proffitt et al. 2003). Deng et al. (2007) also have found genetic differentiation occurred within its populations in China, which might have played an important role in rapid spread of *S. alterniflora*. Bacteria that are associated with establishment and growth of plants can respond rapidly to varying environmental conditions (Gyaneshwar et al. 2002; Rengel and Marschner 2005). Previous studies have suggested that plants from different populations significantly influence the associated soil bacterial communities (Schweitzer et al. 2008; Wardle et al. 2004). We predicted that *S. alterniflora* populations from different geographic sites differentiate their rhizosphere bacterial diversity that is associated with environments of their provenances.

Materials and methods

Seed collection and germination

We collected *S. alterniflora* seeds from nine sites along latitudinal gradient on the east coast of China (Fig. 1; Table 1) in November 2006. In each geographic region, mature seeds were collected from about 100 randomly selected ramets at least 20 m apart from each other to avoid sampling the same clone in the middle marshes and well mixed in plastic bags. The bulk seeds were transported to laboratory and stored at 4°C for further experiments.

In April 2007, 100 seeds from each site were sown into garden soil moistened with 1% NaCl solution in seed trays (50 cm × 35 cm), which were randomly arranged in glasshouse with a natural photoperiod. In mid May, randomly selected six healthy seedlings (7–8 cm tall) from each site were grown in the common garden.

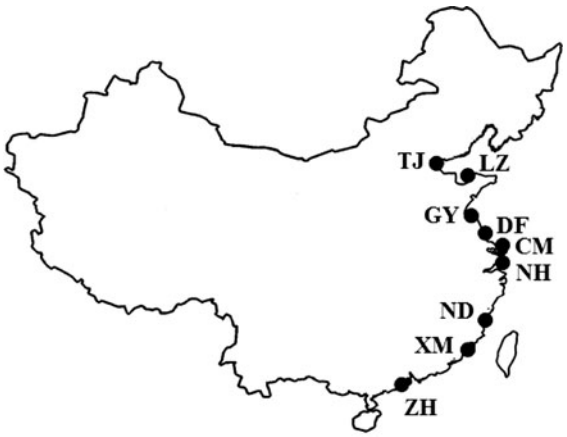

Fig. 1 Map of sampling sites of invasive plant *Spartina alterniflora* along a latitudinal gradient on the east coast of China (TJ, LZ, GY, DF, CM, NH, ND, XM, and ZH). The codes for sampling sites are the same as in Table 1

Table 1 Localities of *Spartina alterniflora* populations collected along a latitudinal gradient on the east coast of China

Sampling points	Latitude	Longitude	Annual mean temperature (°C)
Zhuhai (ZH)	22°26′N	113°39′E	22.4
Xiamen (XM)	24°28′N	117°58′E	21.0
Ningde (ND)	26°37′N	119°37′E	19.3
Nanhui, Shanghai (NH)	30°51′N	121°51′E	15.5
Chongming, Shanghai (CM)	31°31′N	121°58′E	15.3
Dafeng (DF)	33°16′N	120°45′E	14.0
Lianyungang (GY)	34°47′N	119°13′E	13.2
Laizhou (LZ)	37°13′N	119°51′E	12.4
Tianjin (TJ)	39°00′N	117°43′E	12.3

Common garden experiment

The common garden under parallel conditions was set up in the experimental fields of Fudan University, Shanghai of China (E121°30′–N31°18′), consisting of six ponds (3 × 1 × 0.5 m) as blocks. The experiment was designed as randomized complete block (PCB). Seedlings from each site were transplanted into pots (30 cm in diameter and 35 cm in depth) and randomly presented once in each pond. An unplanted pot as control checks (CK) was also presented once in each pond. In one pond, a total of 10 pots (nine planted plots + one unplanted plot) were placed in two rows, and inter-pots distances were, respectively, 25 cm and 13 cm within and between the rows. The fine sandy loam soil for potting was collected from the Fudan University's campus experimental field in Shanghai, China. Each pond was flooded by saltwater of 15 ppt (plants partially submerged, 2–3 cm water above the soil) for simulating common coastal habitats. There are pipelines for linking ponds or draining. We maintained constant salinity by adding fresh water or salt according to salinity which was measured by a standard conductivity meter (S30 Seveneasy Conductivity, Mettler-Toledo, Switzerland). At the beginning of transplanting, each pot was fertilized with 8 g of slow-releasing fertilizer containing 14:14:14 of N/P/K (Osmocote, the Scotts Company, Marysville, OH, USA) for relieving initial nutrient deficiency.

Soil collection

We collected rhizosphere soils of *S. alterniflora* at the late vegetative stage in late September 2007. A parallel study has shown that 12 of 17 plant traits vary significantly among populations of *S. alterniflora* (Zhang et al. 2008). In each pot, rhizosphere soil adhered to the roots was collected (nine populations with a CK in each pond), carefully mixed well in the sterilized plastic bag, and immediately stored at −70°C within half a hour to minimize changes of the samples.

PCR–DGGE

Total genomic DNA was extracted from soil subsamples (6 ponds × 9 populations with a CK) by using the UltraClean Microbial DNA Kit (Mo Bio Laboratories, Inc., Solana Beach, CA, USA) according to the manufacturer's instructions. PCR amplification of bacterial 16S rDNA was performed using the universal primers pair 341F containing a GCclamp (GCGGGCGGGGCGGGGGCACGGGGGGCGCGGCGGGCGGGGCGGGGG) and 907R (Muyzer et al. 1998). The PCR reaction mixture was set up in 50 μl, containing 1 μM of $MgCl_2$, 200 μM of each dNTP, 0.5 μM of each primer, 5 μl of template DNA, 10× PCR buffer, and 2.5U of Ex Taq^{TM} polymerase (TaKaRa Inc., Dalian, China). Touch-down PCR procedure was used for increasing both the specificity and sensitivity of PCR assays in an iCycler thermal cycler (Bio-Rad) (Labbé et al. 2007). After an initial denaturation step for 5 min at 95°C, samples were amplified with denaturation for 1 min at 94°C, annealing for 1 min (temperature decreasing 0.5°C every cycle from 65 to 55°C, and then 15 cycles at 55°C), primer extension for 3 min at 72°C, followed by one final extension at 72°C for 15 min. PCR products from subsamples were pooled on an agarose

gel running at 0.8% agarose gel for 1 h, bands were excised under UV vision for getting rid of nonspecific amplification of PCR, and then DNA was dissolved in 50 µl of elution buffer (10 mM Tris–Cl, pH 8.5) by using the QIAquick Gel Extraction Kit (QIAGEN, Valencia, CA) according to the manufacturer's instructions. 2 µl of the purified product was analyzed by electrophoresis on a 1% agarose gel in 1× Tris–acetate–EDTA buffer (TAE) with ethidium bromide (EB) and visualized under UV light.

Denaturing gradient gel electrophoresis (DGGE) analysis was performed as follows: 25 µl of PCR product was performed with 6% (w/v) acrylamide gels in 1× TAE buffer (40 mM Tris–acetate, 1 mM Na–EDTA, pH 8.0) with a gradient ranging from 20 to 50% (where 100% denaturant was defined as 7 M urea and 40% formamide) at a constant voltage of 100 V and 60°C for 17 h (Bio-Rad Dcode system). The gels were visualized by staining with SYBR green I (1:10,000 dilution of stock solution) for 30 min.

Statistical analysis

The location and intensity of DGGE bands were determined by the Quantity One 4.4.0 software (Bio-Rad) which has been extensively used for analyzing DGGE gels according to the manufacturer's instructions. Shannon–Weaver diversity index (H') was calculated as: $H' = -\sum P_i \ln P_i$, where P_i was calculated as follows: $P_i = n_i/N$, where n_i is the band intensity for individual bands and N is the sum of the intensities of bands on a lane (Girvan et al. 2005). H' method has been reliably responsible for the description of tangible characterization of bacterial diversity, but this approach relies on PCR amplification with its potential biases (Ishii and Fukui 2001). Therefore, we used the H' scores as relative diversity of bacteria. In addition, the number of bands on each DGGE lane was valued as supplement to characterize bacterial diversity. A matrix representing the patterns of bands was used to calculate Pearson correlation coefficient based on the band intensity and location (Siddique et al. 2005). Hierarchical cluster analysis (HCA) was obtained from similarities between the banding patterns by using the unweighted pair group method algorithm (UPGMA) using Multi-Variate Statistical Package (MVSP) 3.1 software (Kovach, UK). Regression analysis was performed to examine the relationship between bacterial community and geographic locality.

Results

Denaturing gradient gel electrophoresis profiles of amplified 16S rDNA fragments from DNA extracted from the rhizosphere bacterial fractions revealed significant differences of the bacterial fingerprints of *S. alterniflora* populations from different geographic locations (Fig. 2). Although the bacterial fingerprints were obtained from the same plant species, the effect of the population provenances was clearly visible based on UPGMA clustering of the PCR–DGGE gels and would be nicely split into separate groups at 59% similarity (Fig. 3). Besides, profiles from the unplanted control were distinctly separated.

The DGGE profiles of rhizosphere bacterial diversity were compared among the *S. alterniflora* populations, and a positive relationship between H'

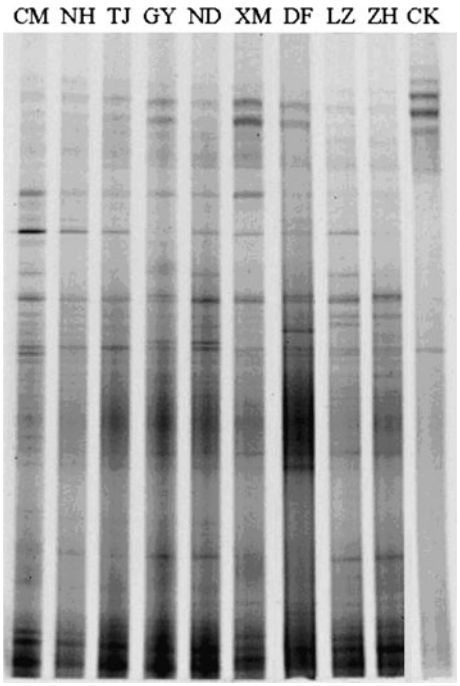

Fig. 2 Denaturing gradient gel electrophoresis of PCR-amplified 16S rRNA gene fragments of rhizosphere bacteria of *Spartina alterniflora* populations (TJ, LZ, GY, DF, CM, NH, ND, XM, and ZH) and the unplanted control check (CK). The codes for sampling sites are the same as in Table 1

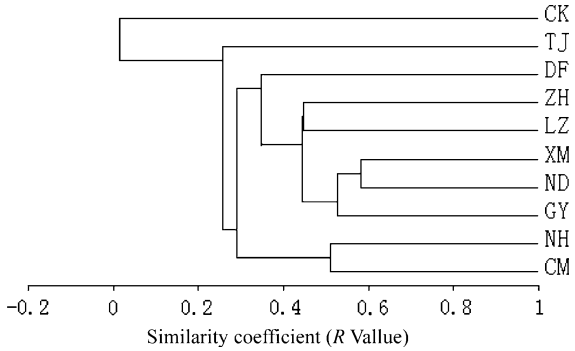

Fig. 3 Dendrogram comparing DGGE fingerprints of rhizosphere bacteria of *Spartina alterniflora* populations (TJ, LZ, GY, DF, CM, NH, ND, XM, and ZH) with those of the unplanted control check (CK). Cluster analysis was performed using the Pearson product moment with unweighted pair group method (UPGMA)

scores and latitude of population provenance was observed (Fig. 4a, $R = 0.674$, $P < 0.05$). Similarly, the number of DGGE bands was positively correlated with latitude (Fig. 4b, $R = 0.711$, $P = 0.015$). These results illustrated that rhizosphere bacterial diversity of *S. alterniflora* populations from invaded ecosystems increased with latitude.

Discussion

Our study provides evidence that the population variation of invasive plant *S. alterniflora* in response to growing conditions of different invaded geographic regions had significant effects on rhizosphere bacterial diversity. We observed that rhizosphere bacterial diversity of *S. alterniflora* populations increased with increasing latitude of population provenance on the east coast of China. This result indicates that in the common garden experiment variation within *S. alterniflora* populations shaped specific plant–soil bacterial diversity relationship, which corresponded to a latitudinal gradient in the invaded ecosystems.

The latitude constitutes a complex environmental gradient, determining available energy and nutrient recourses, temperature or temperature variability, heterogeneity of soil conditions (Li et al. 1998), all of which contribute to population differentiation which in turn facilitates invasive plants to adapt to novel environments (Sax 2001). Previous studies

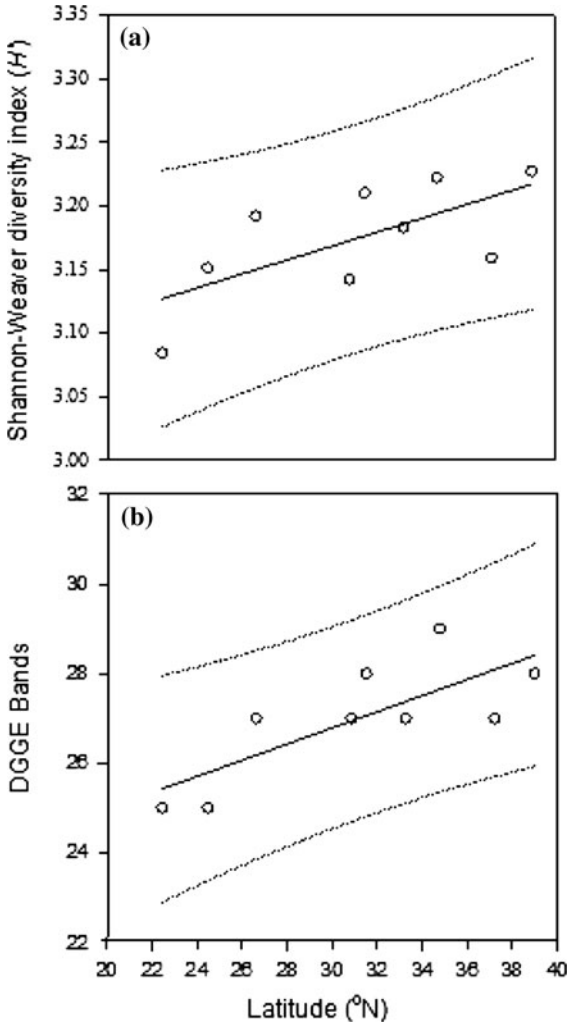

Fig. 4 The relationships between the latitude of population provenance and **a** the value of the Shannon–Weaver diversity index (H'), and **b** the number of DGGE bands of rhizosphere bacteria of *Spartina alterniflora* populations along a latitudinal gradient on the east coast of China. The fitted equation are $y = 3.005 + 0.00543 \times$ ($R = 0.674$, $P = 0.046$) (**a**) and $y = 21.406 + 0.180 \times$ ($R = 0.771$, $P = 0.015$) (**b**)

have suggested that novel abiotic environments such as salinity, temperature, soil nutrition, and solar radiation, together with novel biotic environments such as new neighbors, have profound impact on the population differentiation of *S. alterniflora* (Proffitt et al. 2005; Proffitt et al. 2003; Seliskar et al. 2002). In the invaded ecosystems of China, latitude also is an important determinant of environmental conditions that contribute to population differentiation of *S. alterniflora* (Zhang et al. 2008). Above results suggest that *S. alterniflora* has great potential of

adapting to the invaded environments which have close relation with its population variation.

At the level of plant ecotype or genotype, many short-term experiments have suggested that population variation of plants has considerable impacts on microbial diversity and functions (Madritch and Hunter 2002; Schweitzer et al. 2008; Seliskar et al. 2002). The variation of quantity and quality of plant exudates among plant populations might make it possible to change microbial community because plant exudates determine substrate availability for soil microbes (Schweitzer et al. 2008). Previous studies have indicated that *S. alterniflora* is known as a 'keystone' resource for soil biota in salt mashes along latitudinal gradient. Rhizosphere microbial respiration of *S. alterniflora* from high latitude was higher than that from low latitude (Seliskar et al. 2002). This result was consistent with our observations because of close relationship between microbial diversity and activities associated with microbial respiration.

Low-latitude areas have higher temperature, which speeds up metabolic activities, cell growth, primary productivity, and hence growth of the whole plant. At the high latitude, plants experience low temperature and short growing season. However, the plants from high latitude have great potential to respond positively to increasing temperatures, such as great photosynthetic potential and growth rate (Arft et al. 1999; Tranquillini 1964). In a common experiment, Zhang et al. (2008) have found that *S. alterniflora* populations from high latitude have greater growth rate of plant height and shorter growing season than those from low latitude because of genetic differentiation in response to increasing latitude. The plants from high latitude can input more exudates from photosynthesis into soil which activate rhizosphere bacteria compared to the plants from low latitude under the some conditions (Horner-Devine et al. 2003). Therefore, different growth rates of *S. alterniflora* at different latitudes may allow for the clinal relationship between population variation of *S. alterniflora* and its rhizosphere bacterial diversity. Because high bacterial diversity can improve the soil functions and nutrient acquisition of plants (Gyaneshwar et al. 2002; Nannipieri et al. 2003; Seliskar et al. 2002), the association between *S. alterniflora* and its rhizosphere bacteria may play an important role in its adaptations to high-latitudinal environments and enhancing its invasiveness.

Many studies have shown that plant–soil biota feedbacks enable invasive plants to become effective invaders in the invaded ecosystems (Reinhart and Callaway 2006; Wolfe and Klironomos 2005). Different geographic populations of *S. alterniflora* have varying impact on ecosystem functions, such as microbial respiration and edaphic chlorophyll (Seliskar et al. 2002). Further work can be directed towards the understanding of what roles the specific plant-soil bacterial diversity relations play in the successful invasions of *S. alterniflora* across a wide range of latitudes.

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