



Original article

Temporal priority effects on competition are not consistent among intermountain grassland species

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ARTICLE INFO

Article history:

Received 22 February 2016

Received in revised form

23 June 2016

Accepted 11 July 2016

Available online 18 July 2016

Keywords:

Gram per gram competitive effect

Native species

Priority effect

Relative interaction

Root: shoot ratio

ABSTRACT

Previous work indicates that priority effects exist, but mechanisms are not well understood. So we explored shifts in competitive outcomes and intensities as a potential general mechanism. In a standard greenhouse experiment the temporal priority effects of the target species *Pseudoroegneria spicata* and its competitive responses to five receptor species, i.e., *Bromus ciliatus*, *Bromus marginatus*, *Coreopsis tinctoria*, *Senecio atratus*, and *Solidago canadensis* were evaluated. *P. spicata* adults with a high root: shoot ratio had a significant inhibitory priority effect on *B. ciliatus*, *B. marginatus*, and *C. tinctoria*. Compared with the target species, under later and simultaneous sowing, *B. ciliatus*, *B. marginatus*, *C. tinctoria*, and *S. atratus* exhibited an increasing trend in terms of competition. However, *S. canadensis* did not display priority effects. In addition, the gram per gram competitive effect of *P. spicata* depended on the receptor species in the following order: *B. marginatus* > *B. ciliatus* > *C. tinctoria* > *S. atratus*. There were positive relationships between the relative interaction indices and the root: shoot ratios in *B. ciliatus*, *B. marginatus*, and *C. tinctoria*, thereby suggesting that the early germination or emergence of *P. spicata* may reduce the root: shoot ratios of these receptors. The results of this study indicate that priority effects occurred in early colonizers with high root: shoot ratios and greater competitive capacities.

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1. Introduction

In ecological communities, the particular effects of species on each other often depend on the arrival order or seed germination speed, which are known as “priority effects” (Connell and Slatyer, 1977). Thus, early settlers can significantly inhibit or stimulate species arriving later (Young et al., 2005). In a field experiment where an annual grass invaded a shrub-steppe ecosystem in eastern Oregon, Schantz et al. (2015) discovered that applying a priority effect from perennial grass by delaying annual grass seeding until spring initially facilitated the establishment of the perennial grass, although this effect did not persist into the second growing season. Plücker et al. (2013) found that the species that arrived first at a disturbed site played a key role in the subsequent development of the community, where this priority effect

influenced the aboveground productivity, species diversity, and stability of the developing grassland community. Moreover, priority effects may vary among species and environments. For example, the priority effect was shown to be very strong among representative species inhabiting a wide ecological niche (Vannette and Fukami, 2014). Cleland et al. (2015) found that the role of seasonal priority effects varied among species, and that native species could benefit from seasonal priority effects in restoration efforts even when in competition with fast-growing exotic annual species. Thus, priority effects may depend on life history processes and disturbance events at different spatial and temporal scales (Munguia et al., 2010).

Numerous studies have attempted to understand priority effects in ecosystems. Grman and Suding (2010) discovered that size-asymmetric competition and soil legacies led to priority effects by plants. In addition, succession theory implicitly recognizes priority effects, where the earlier arrival of certain species has important impacts on the future composition of a community (Tansley, 1935). Furthermore, Kennedy et al. (2009) found that the timing of colonization had a significant effect on the outcome of competition

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between two ectomycorrhizal fungi in the genus *Rhizopogon*, where the species that colonized first always achieved competitive dominance. Martin and Wilsey (2012) concluded that a priority effect drove the community assembly and that altering priority effects during the assembly history had a major influence on the subsequent species composition and diversity. Byun et al. (2013) found that fast-growing annuals had the highest relative competition index, thereby suggesting a priority effect. During ecological invasion process, many contemporary studies ignored the role of density-dependent priority effects, and thus failed to assess major differences between movement and establishment. So priority effects can lead to underestimation of dispersal and invasion potential (Fraser et al., 2015).

Priority effects have important implications for ecological restoration (Young et al., 2005). In particular, in an ecosystem dominated by invaders, information about priority effects can help ecosystem managers to identify cost-effective strategies for improving the survival, persistence, and biotic resistance of native species with inferior competitive capacities (Chadwell and Engelhardt, 2008). In addition, priority effects included positive and negative interaction within and between species, which possibly depended on population densities and thus affect

alternative stable states and alternative endstates of community assembly (Gerla and Mooij, 2014). However, little is known about how priority effects in native plants might influence their competitive abilities and growth performance. In the present study, we performed a greenhouse experiment to determine whether temporal priority effects exist in six native plants from an intermountain grassland habitat. In addition, we also tested the competitive effects of the target species *Pseudoroegneria spicata* on the other five species as receptors, as well as determining the root:shoot ratios of these native species. We aimed to explore the shifts in competitive outcomes and their intensities as a potential general mechanism related to priority effects.

2. Materials and methods

2.1. Materials

This experiment was conducted in a greenhouse at the University of Montana, Missoula, MT, USA. Seeds were sown or seedlings were grown in cylindrical pots, which measured 7.5 cm in diameter and 23 cm in height. The bottom of each pot was filled with 100 mL of silica sand, over which 400 mL of a homogenized mixture of field

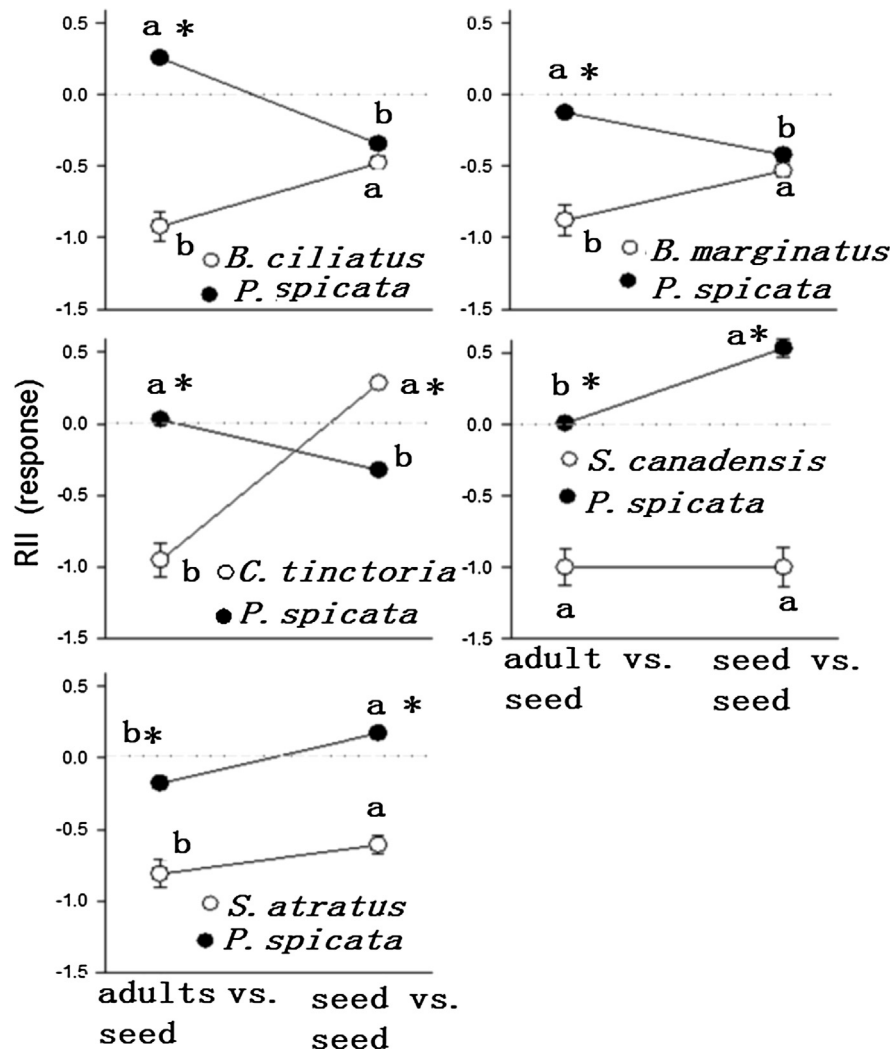


Fig. 1. Interactions between the target species *Pseudoroegneria spicata* and the five receptor species. The white circles denote the receptor species and black circles represent the target species. Each pair of *P. spicata* and a receptor was tested in adult vs. seed and seed vs. seed treatments. In each treatment, we calculated the relative interaction index (RII) for both the target and receptor species. The average RII values are shown with the standard error ($n = 12$). Small letter meant significant difference between both treatments on the same species ($p < 0.05$). Asterisk (*) meant significant difference between both species on the same treatment ($p < 0.05$).

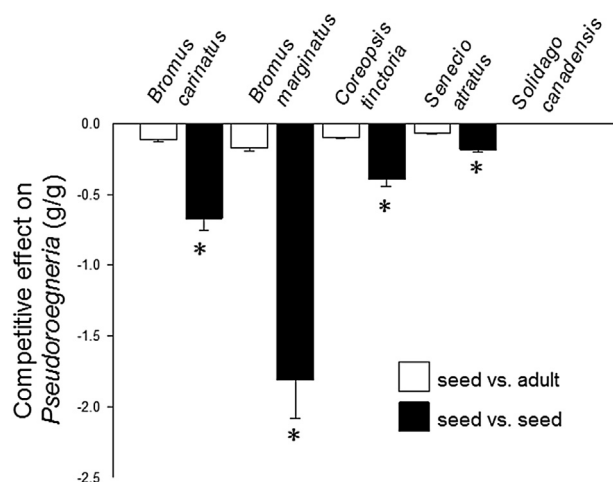


Fig. 2. Competitive effects of the five receptor species on the target *Pseudoroegneria spicata*. The gram per gram competitive effect of the receptor species on the target species was calculated as: (treatment for the target species – control for the target species)/treatment for the receptor species, based on the biomass values. Standard errors and the means are shown. The seed vs. adult and seed vs. seed treatments refer to the receptor species vs. the target species, respectively. Except for *Solidago canadensis*, all comparisons are very significant ($p < 0.05$). Asterisk (*) meant significant difference between both treatments on the same species ($p < 0.05$).

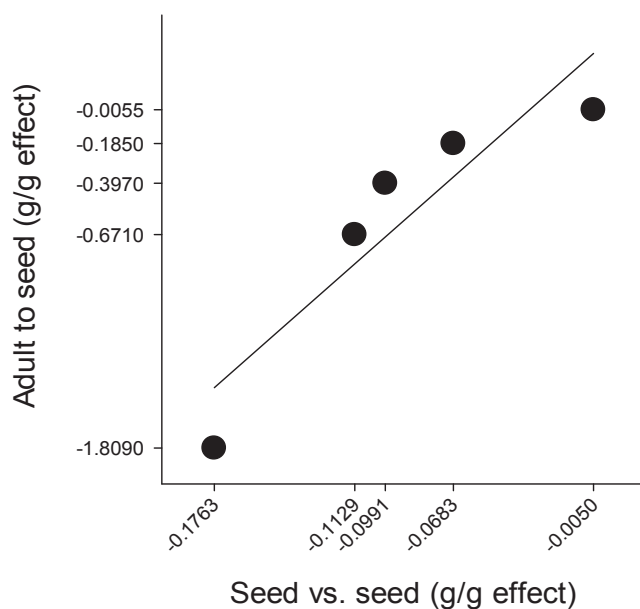


Fig. 3. Relationships between the competitive effects of the five receptor species in seed vs. seed and adult vs. seed pairings. The seed vs. adult and seed vs. seed treatments refer to the target species vs. the receptor species, respectively. The values marked on X and Y axes reflect the gram per gram competitive effect of the receptor species on the target species in seed vs. seed and adult vs. seed pairings, respectively ($r = 0.8785$, $p < 0.05$).

soil from a local intermountain grassland and silica sand was added at a 1:1 ratio. In this experiment, five representative plant species were selected as test receptors, i.e., *Bromus ciliatus* (perennial grass), *Bromus marginatus* (Mountain brome grass), *Coreopsis tinctoria* (annual Asteraceae forb), *Senecio atratus* (perennial Asteraceae forb), and *Solidago canadensis*. *S. canadensis* is a herbaceous perennial plant of the family Asteraceae native to northeastern and north-central North America but established as an invasive plant in other parts of the continent and in other countries as well ([https://](https://en.wikipedia.org/wiki/Solidago_canadensis)

en.wikipedia.org/wiki/Solidago_canadensis). In addition, *P. spicata* as a dominant species of grass in local community of Montana State of USA, known by the common name bluebunch wheatgrass, was used as a target species to assess its priority effects and the competitive abilities of the other five species mentioned above. These five receptors are distributed sporadically in the community colonized by the target species *P. spicata*.

2.2. Experimental design

To test for priority effects, we varied the timing of seed sowing in an array of treatments. In the priority effect treatment, we co-cultured the adult of the target species at about two months after seed germination with one active seed of each receptor species in a pot. In addition, one seed from the target species and another seed from a receptor species were also co-cultured in a pot, which was used as the control.

The initial target species were sown on June 16, 2013, whereas the subsequently sown receptor species and all controls were sown on August 15, 2013. We used 264 pots in the experiment, with 12 replicates of each treatment ($[5 \text{ species} \times 2 \text{ treatments} \times 12 \text{ replicates}] + [6 \text{ species} \times 2 \text{ control} \times 12 \text{ replicates}] = 264 \text{ pots}$). During the experiment, all of the pots were watered once each day. Sufficient lighting was provided for 12 h as daylight from June 16, 2013 until the end of the experiment. A randomized block design was also employed where each of the 12 replicates was located in a different section of the greenhouse table. Plants were harvested from October 28–29, 2013, cleaned and divided into the aerial parts and roots, dried respectively for 72 h at 105 °C, and the biomass of the aerial part and roots in each replicate, was then recorded by the Analytical Balance, respectively. The total biomass was finally calculated. The mean of each treatment was acquired by averaged twelve replications by SPSS 17.0 ($n = 12$). The determination methods were shown in Luo et al. (2016).

2.3. Statistical analyses

In our experiments, according to the methods described by Callaway et al. (2002) and Armas et al. (2004), the improved relative interaction index (RII) for the target and receptor species was calculated as: (biomass of treated – biomass of control)/biomass of control. The treatment and control were considered to represent growth with other plants and alone, respectively. Intuitively, the RII ranges from -1 to $+\infty$, where negative values indicate competition and positive values denote facilitation. We analyzed all of the data by SigmaPlot 12.5 using two-way analysis of variance with a randomized block design. Meanwhile Pearson's correlation analysis was conducted to verify the findings consistence between both treatments: adult to seed and seed to seed on the gram per gram competitive effect. Furthermore, ANOVA, Tukey's Test for multiple comparisons and significant differences analyses were conducted by SPSS 17.0.

3. Results

3.1. Temporal priority effects and competition among the target species and five receptors

The target species *P. spicata* had a priority effect ($p < 0.05$), which depended on the receptor species. From adult to seed, *P. spicata* exhibited a decreasing effect in competition on *B. ciliatus*, *B. marginatus*, and *C. tinctoria*. Similarly, from later to early seed sowing, the competition between *B. ciliatus*, *B. marginatus*, and *C. tinctoria* with *P. spicata* tended to increase, and thus these three species also had priority effects ($p < 0.05$). However, *S. canadensis*

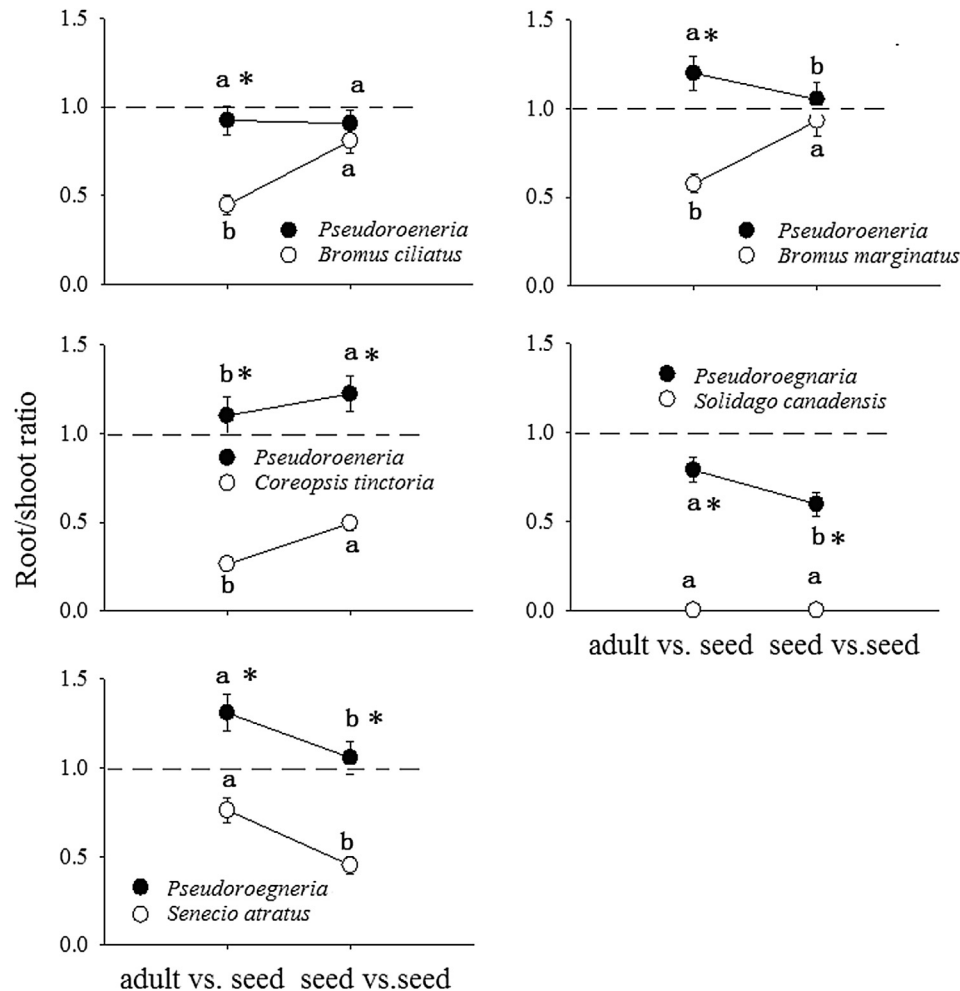


Fig. 4. Root:shoot ratios of the receptor species and the target species *Pseudoroegneria spicata*. *Pseudoroegneria spicata* was abbreviated to *Pseudoroegneria* in Fig. 4. The white circles denote the receptor species and black circles represent the target species. The seed vs. adult and seed vs. seed treatments refer to the target species vs. the receptor species, respectively. The average root: shoot ratios are shown with the standard errors ($n = 12$). Small letter meant significant difference between both treatments on the same species ($p < 0.05$). Asterisk (*) meant significant difference between both species on the same treatment ($p < 0.05$).

did not display priority effects (Fig. 1). Four receptor species, i.e., *B. marginatus*, *B. ciliatus*, *C. tinctoria*, and *S. atratus*, had significant competitive effects on *P. spicata* ($p < 0.05$). Furthermore, the competitive effects were stronger in the seed vs. seed combinations than those in the seed vs. adult combinations, where the strength of competition decreased in the order of: *B. marginatus* > *B. ciliatus* > *C. tinctoria* > *S. atratus*. However, *S. canadensis* had no competitive effect on *P. spicata* (Fig. 2). There was a significant positive relationship between the competitive effects in the adult vs. seed and seed vs. seed combinations ($r = 0.8785$, $p < 0.05$). The gram per gram competitive effect of the receptor species on *P. spicata* was consistent in both treatments (Fig. 3).

3.2. Root: shoot ratios in *P. spicata* and the receptor species

In both treatments, i.e., adult vs. seed and seed vs. seed, the root: shoot ratios depended on the species and the pairing. The root: shoot ratio profile for the pairing of *P. spicata* and *B. ciliatus* was similar to that for *P. spicata* and *B. marginatus*. The root: shoot ratio of *P. spicata* only exceeded 1.0 in the pairing of *P. spicata* and *B. marginatus*. In the adult vs. seed pairings, the root: shoot ratio of *P. spicata* exhibited a decreasing trend. By contrast, in the seed vs.

seed pairings, the ratios increased for *B. ciliatus* and *B. marginatus*. However, the root and shoot biomasses of *S. canadensis* in the seed vs. seed pairings were so small that the root: shoot ratio was close to zero (Fig. 4).

4. Discussion

4.1. Priority effects among native plant species from an intermountain grassland habitat

Priority effects are very common in plant ecosystems. Moore et al. (2012) found that arriving at a site earlier played a major role in the colonization success of *Polygonum persicaria*. In the present study, the target species *P. spicata* exhibited a stronger competitive capacity during the adult period than the seed or seedling stages ($p < 0.05$). In addition, *B. ciliatus*, *B. marginatus*, *C. tinctoria*, and *S. atratus* exhibited greater competitive capacities when sown early compared with late seed sowing ($p < 0.05$). Compared with late sowing, their competitive intensity with early sowing was enhanced by 93%, 65%, 194%, and 33% in the four receptor species, i.e., *B. ciliatus*, *B. marginatus*, *C. tinctoria*, and *S. atratus*, respectively. Thus, our results demonstrate that the arrival time of a plant species affected its physiological response

and competitive ability. Especially, Asteraceae forbs had stronger competition than grasses (Figs. 2 and 3). Geange and Stier (2010) proposed that both the habitat complexity and priority effects can influence the competitive strength of species.

4.2. Mechanisms that mediate priority effects in competition by natives and root:shoot ratios

In the present study, we found that the receptor species with early seed sowing or early germination had stronger competitive capacities and higher root: shoot ratios, which might explain their priority effects. The size-asymmetric competition can lead to priority effects (Grman and Suding, 2010). In particular, there were significant positive relationships between the competitive capacities and root:shoot ratios of *P. spicata*, *B. ciliatus*, and *B. marginatus*, which suggests that their physiological traits might explain the priority effects. Byun et al. (2013) found that annual wetland plants with more rapid growth had high relative competition indices, and thus they had priority effects in their specific niche depending on the functional group considered.

S. canadensis did not display priority effects and competitive advantage, which implied that it failed to benefit from reduced priority effects. Pal et al. (2015) found that *S. canadensis* exhibited weaker competition and allelopathic in the native range than in the non-native range.

4.3. Potential application of priority effects in plant communities

In the present study, we found that early sowing of the target species *P. spicata* led to strong competitive dominance and inhibited the growth of five selected receptor species, which were sown later. Similarly, the early sowing of the receptors resulted in inhibitory priority effects on the target species. Therefore, the priority effects of natives may have great potential for applications in biological resistance to exotic invasive species and restoration ecology. Martin and Wilsey (2012) suggested that the establishment of native species before exotics may allow them to become fully dominant, thereby facilitating the efficient implementation of ecological restoration. In addition, Plückers et al. (2013) found that the priority effects obtained by the early sowing of two different seed mixtures could rehabilitate dry acidic grassland with a sandy substrate.

Studies have shown that species that arrive first at a disturbed site can play a key role in the subsequent development of the community, where this priority effect influences the aboveground productivity, species diversity, and stability of developing grassland communities (Gerla and Mooij, 2014). Inhibitory priority effects have many applications in ecological regeneration (McCormick and Poulos, 2014) but we should also consider the importance of facilitative priority effects in future research.

5. Conclusions

In this study, given the general importance of priority effects in ecological system, we focused on their applications in ecological restoration and biological resistance to exotic invaders. At present, ecologists do not fully understand the nature, mechanism, and meaning of priority effects in plant communities. Thus, we explored shifts in the competitive outcomes and intensity as a potential general mechanism to explain priority effects. We found that both *P. spicata* and the receptors exhibited priority effects, which indicates that priority effects are very common in plant communities. In particular, the early sowing of *B. ciliatus* and *B. marginatus* resulted in strong competition and high root: shoot ratios. Thus,

early settlers might have a competitive advantage, which has great implications for plant communities and ecosystems. However the poor competitors like *S. canadensis* did not take advantage of priority effects. In future research, it will be necessary to investigate other mechanisms in addition to competition, as well as obtaining field evidence for priority effects.

Acknowledgement

We appreciate the helps of Róbert Pál, David Hooper, Huixuan Liao, Wenbo Luo, Qingquan Ni, Yingji Zhao, Jacob Lucero, Nicole Hupp, and Mandy Slate during lab work, greenhouse experiment. This study was supported by Key Projects of The Outstanding Young Talents in Colleges and Universities (gxyqZD2016024), and China Scholarship Council ([2012]3022), Anhui Province, and Ministry of Human Resources and Social Security of the People's Republic of China (MOHRSS) for studying abroad (013).

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