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교육학석사 학위논문

**Study on the life historical strategy of
an early successional species
(*Penthorum chinense*) for restoration**

**천이 초기종인 낙지다리의 복원을 위한 생활사
전략에 대한 연구**

2016년 2월

서울대학교 대학원

협동과정 환경교육전공

양 윤 영

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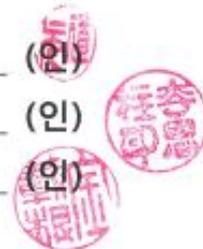
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ABSTRACT

Study on the life historical strategy of an early successional species (*Penthorum chinense*) for restoration

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Translocation into new habitats is an essential way to conserve rare plant species. The common failure of this effort stems predominantly from unsuitable new habitats. I performed a field survey and mesocosm experiments in order to understand the realized niche, fundamental niche, and tolerance to environmental conditions of *Penthorum chinense* for the successful translocation of the sandy riparian rare plant, *P. chinense*. Environmental range for the distribution of *P. chinense* is characterized by a relatively low degree of succession (9.02~1031), high percent photosynthetically active radiation (11.94~100 %), low contents of soil organic matter (0.89~4.38 %), NO₃-N (0.04~12.61 mg kg⁻¹), and PO₄-P (0.75~28.42 mg kg⁻¹), much sand (13.85~94.98 %) among the soil texture classes, and low water depth or watersides (-9~7 cm) with a wide range of water content

from waterlogged soils to dry soils of the water-level-fluctuation zone. All the individual plants survived, grew, and reproduced both asexually and sexually under all treatments except extreme low light (ELL) group. In addition, the seed number and final germination percentage of *P. chinense* did not drastically decrease, even during severe stress except low light (LL) group in our experiment. The result indicated that *P. chinense* has a narrow realized niche which requires oligotrophy and disturbance, even though the fundamental niche of the soil nutrient and water content appears to be large. Also, *P. chinense* showed a variety of traits tolerant to nutrient deficit, drought, waterlogging, and submergence of 15 days. The restricted distribution of *P. chinense* to low-productive peripheral habitats might be a strategy to reduce competition for light, which occurs frequently with other rare plant species as well, and *P. chinense* has the strategies to increase survival in habitats that have alternate occurrences of flooding and drought. Here, I suggest that *P. chinense* be translocated to sandy soils that include gravel in waterside environments or shallow waters with periodic flooding, where low nutrients and water holding capacity cause reduction in the competitor's performance; on the other hand, *P. chinense* has the ability to tolerate these conditions. I believe that my research could be a good starting point for study of the translocation of rare plants to suitable sites.

Keywords : Fundamental niche • Gravel • *Penthorum chinense* Pursh • Realized niche • Reintroduction • Tolerance • Translocation

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1. Introduction

Biodiversity promotes the efficiency for ecological communities to capture biologically vital resources, to produce biomass, to decompose and to recycle biologically essential nutrients (Cardinale et al. 2012). Biodiversity also increases the resistance to invasion by exotic plants as well as aboveground carbon sequestration. In addition, plant pathogens are less prevalent in more diverse plant communities (Cardinale et al. 2012). However, human activities currently cause dramatic losses of species and these extinctions result from a variety of causes, including habitat modification and destruction, biological invasions, and climate change (Lavergne et al. 2005). Management of intact ecosystems and restoration of degraded ecosystems are seen as critical to the protection of both biodiversity and ecosystem services in this period of strong human alteration of ecosystems (Hobbs and Cramer 2008).

Rare plants are under increasing risk of extinctions in natural habitats. Rare plant species need to be conserved because a number of rare plant species are constant components of diverse vegetation communities and food plants for specialist invertebrate species of conservation importance (Pywell, Bullock et al. 2003). It is widely accepted today that the strategies for conservation of rare plants are in situ and ex situ conservations (Heywood and Iriondo 2003). In restoration of rare plant species, an array of techniques is available, including seed storage, tissue culture, germination enhancement, and translocation (Hobbs and Cramer 2008). Especially, the translocation of new populations is an essential method associated with the conservation of rare plant species; IUCN (1987) defined 'translocation' as any movement of living organisms from one area to another, and recognized three types of translocation: introduction, reintroduction, re-stocking. This is because the spontaneous recovery of rare plant populations on restored sites may be constrained by the minimal natural occurrence of propagules as many plants have transient seed banks and many are dispersal-limited (Godefroid et al. 2011). Thus,

plant translocation reduces the risk of extinction of rare plant species, and such strategies have become increasingly important in conservation worldwide (Heywood and Iriondo 2003).

However, in the few cases of efforts in plant translocation that have been evaluated systematically, results showed that only a small percentage was successful. The common failure of these efforts stems from predominantly unsuitable habitats for the translocated plants (Godefroid et al. 2011). Zedler (2000) suggested that species be planted in suitable microsites for biodiversity of restored wetlands. Selecting a suitable habitat for translocated plants will minimize environmental stresses, and continued survival of translocated material will depend on favorable environmental conditions (Hobbs and Cramer 2008). Thus, the detailed information of the habitat requirements of rare plant species must first be gathered for the successful translocation. Without any research of habitat needs, these efforts might be high-risk and high-cost activities. The study of appropriate sites for translocating rare plant species is therefore crucial.

Niche-differentiation mechanisms indicate that plants segregate along various environmental niche axes, including gradients of light, root depth, soil moisture, and nutrients (Silvertown 2004). This plays an important role in the coexistence and stabilizing of species diversity. Niches comprise two types: the realized niche which a species is able to occupy in the presence of competition and natural enemies, and the fundamental niche which a species is able to occupy in the absence of competition and natural enemies (Levine and HilleRisLambers 2009). In addition, each plant species has a variety of tolerance developed by surviving through the various types and intensities of stress and disturbance in their habitat (Grime 1977). To understand a species' capacity to persist in stressful environments, it is important to understand their tolerance for resource limitation. A suitable traits should lead to individual plant survival, continued vegetative growth, and generative reproduction.

Hence, to understand the realized niche, the fundamental niche and tolerance to environmental conditions of rare plant species have essential when translocating these plants. Previous reports of rare plant species are mostly focused on reproductive and genetic traits. However, only a few studies have reported the realized niche, the fundamental niche and tolerance to environmental conditions of rare plant species. The data of rare plant species will provide the baseline information for suggesting suitable sites for translocation, and will thus be useful for conserving these plants and preventing their extinction. The problems caused by executing the access to the limited or inadequate data are very serious, and our society should be made aware of the importance of allocating resources to gather such baseline information on rare plant species (Heywood and Iriondo 2003).

Wetlands are a major type of ecosystem affected by humans, and they are currently in the process of being restored. Typical wetland succession is initiated by a partial or total disturbance (Platt and Connell 2003), and the position of the wetland's reset point, which is initial point of life cycle with partial or total disturbance occurred in this wetland communities, is a key factor in the biodiversity of wetlands (Zweig and Kitchens 2009). Data in Costanza et al. (1998) indicate that 40% of global renewable ecosystem services are provided by shallow waters. Generally, wetland restoration aims to restore lost biodiversity or provide services, such as flood-peak reduction, water quality improvement (Zedler 2000), and the dollar value of wetland functions is particularly high.

I selected *Penthorum chinense* Pursh, a rare plant species that inhabits the position of the reset point in wetlands. The habitat of *P. chinense* was surveyed at 10 sites in riparian flood plains, marshes, wetlands around paddy fields, and abandoned paddy fields by Shin (2011), at 19 sites in riparian flood plains, wetlands around paddy fields, and abandoned paddy fields by Kang et al. (2003) and 1 site in abandoned paddy fields by Ohkuro et al. (2003). Because it was considered that *P. chinense* population is predominantly occurred and become self-sustaining for a long time at reset point by periodic disturbance, I selected three

riparian flood plains in upper region of a river, midstream and downstream. And I surveyed essential variables to propose the suitable sites for translocation of *P. chinense* due to insufficient data of the previous studies. In this study, I researched the environmental range for the distribution of *P. chinense* in field to understand the realized niche of *P. chinense*, and conducted laboratory experiments of soil nutrient content, soil water content, submergence, post-submergence and light intensity to figure out the fundamental niche and tolerance to each environmental condition of *P. chinense*. And I proposed the most valid sites for the translocation of *P. chinense* on the basis of the results of our study. My paper might be a good example of a combination of field and laboratory studies to determine suitable environment for the translocation of rare plants.

2. Materials and methods

2.1 Study species

P. chinense is distributed in eastern Asia and is similar to *P. sedoides* L., which is native to the eastern half of the U.S.A. (Haskins and Hayden 1987). The plant is often distributed in riparian flood plains, marshes, wetlands around paddy fields, and abandoned paddy fields, and reproduces both sexually by seeds and vegetatively by rhizomes (Yonemura 2000; Ikeda and Itoh 2001). This species has been utilized as a component of the Chinese medicine, Gansu grain, which has healing effects such as reducing the level of tansaminase and protecting the liver and spleen (Cao et al. 2007). Currently, the *P. chinense* population has been decreasing due to habitat destruction caused by river improvement, wetland reclamation, and reduction of traditional agricultural practices (Ikeda and Itoh 2001). Thus, it was listed as least concerned species in Korea (Korea Forest Service 2014) and as a vulnerable species in Japan (Japanese Ministry of the Environment 2014).

2.2 Field survey

2.2.1 Vegetation survey

I selected three riparian flood plains, Yongin, Paju, and Hongsung (Table 1; Fig. 1). I established fifteen 2×2 m² quadrats at Yongin, sixteen quadrats at Paju, and twelve 1×1 m² quadrats at Hongsung according to the *P. chinense* community size (total 43 quadrats). Each quadrat was classified into three groups according to importance value of *P. chinense* : many *P. chinense* shoots (group 1; Yongin 8 samples, Hongsung 4 samples), a few or absent (adjacent to) of *P. chinense* shoots (group 2; Yongin 7 samples, Paju 16 samples), and its pure stands (group 3; Hongsung 8 samples). I measured the cover, density, and height of all plant species in 2012 during the growing season (May ~ July), based on a modification of the Braun–Blanquet plant sociological method (Mueller and Ellenberg 1974).

2.2.2 Photosynthetically active radiation measurement

In each quadrats, I measured photosynthetically active radiation (PAR) just above the top of *P. chinense* plant and PAR of full light at the open air surrounding nearly at the same time (researched one *P. chinense* plant or 4 different *P. chinense* plants within each quadrats). Moreover I measured PAR at height of 10 cm from the soil surface at quadrats absent (adjacent to) of *P. chinense* shoots with large size plant species and PAR of full light at the open air surrounding nearly at the same time. PARs were measured using a Li-Cor quantum meter (Model Li-250A; Li-Cor Biosciences, Lincoln, Nebraska, USA). I analyzed percent PARs; The *percent PAR (field)* = PAR of respective quadrats / PAR of full light at the open air surrounding.

2.2.3 Water level measurement

I measured the depth of the water, which was defined as the distance from the water table to the soil surface; the depth of the water was positive when the soil surface was below the water table and negative when the soil surface was above the

water table. I was not able to measure the depth of water for quadrats that is located away from the stream when I surveyed at field. However I assured that the quadrats were in low lands relatively closed to the stream and were sunk under water in flood time. When the quadrats were submerged under flood waters in July, I measured the depth of the water and current velocity using current velocity meters (Flow Captor Type 4311.30, Weber Sensors, Inc.).

2.2.4 Substrate analyses

The substrate samples were collected from the root layer (10 cm below the surface) adjacent to each quadrat not to damage vegetation of quadrats. The number of the substrate samples was less than the number of the quadrats, because I collected substrate specimen from group of quadrats that are very near each other with narrow distribution area of *P. chinense*. I passed these samples through a 2 mm sieve (standard sieve #10) and determined the soil texture using the hydrometer analysis method and a texture triangle (Sheldrick and Wang 1993). The organic matter content was assessed using the loss on ignition method (John 2004). The total volume of water in wet soil was measured as fresh soil moisture immediately after passing it through a sieve by oven drying at 105°C for ≥ 24 hours. The soil pH was measured in a water/substrate suspension (1:5 w/v). NO₃-N was extracted with 2 M KCl solutions and measured using the hydrazine method (Kamphake et al. 1967). PO₄-P was extracted with Bray No. 1 solution (Bray and Kurtz 1945) and measured using the ascorbic acid reduction method (Solorzano 1969).

2.2.5 Water analyses

I collected water samples. The pH and turbidity of this water was measured with a pH meter (model AP 63; Fisher, Pittsburgh, PA, USA) and with a turbidimeter (Hach 2110P; Hach Co., Loveland, Co, USA), respectively. I filtered collected water with a membrane filter (pore size, 0.45 μ m) and NO₃-N and PO₄-P

were analyzed by the hydrazine method (Kamphake et al. 1967), and ascorbic acid reduction method (Solorzano 1969), respectively.

2.2.6 Soil profiles including gravel analysis

The soil profiles (20 cm wide, 20 cm long, and 10 cm deep) were prepared in 3 locations at Youngin. The soil mass was sieved through a 2 mm mesh sieve and coarse fragments larger than 2 mm were further sieved through 6, 10, and 20 mm sieves and separated. Fragments larger than 20 mm were hand separated in size groups of 20-40, 40-50, 50-80, and larger than 80 mm diameter (including gravel) at the longest axis. Each coarse fragment sample was washed in water, air dried and weighed.

2.2.7 Data analyses

I calculated the importance value, Shannon–Wiener index, and degree of succession for the vegetation data in each quadrat. Relative density (RD) and relative cover (RC) were used to determine the importance value ($IV = (RD + RC)/2$). Species diversity was calculated as the Shannon–Wiener index, $H' = -\sum_{i=1}^n (p_i \log p_i)$, where $p_i = n_i/N$; n_i = number of individuals of a species i and N = total number of individuals. The degree of succession was calculated from the equation, $DS = (\sum_{i=1}^n dl/n) v$, where l is the categorized life span of each species related to Raunkier's life-form, e.g. MM and M=100; N=50; Ch, G and H=10; Th and Th (w)=1, with the exception of the *P. chinense* in Hongsung because I was assured that the plants were one year old. Here, n is the number of species in a quadrat and v is the vegetation coverage of each quadrat. $d = (C' + H')/2$; $C' = (c/c_{max}) \times 100$; $H' = (h/h_{max}) \times 100$, where c and h are the cover and height of each species, respectively (Kitazawa and Ohsawa 2002).

Table 1 Location and habitat type of study sites.

Site name	Geographical coordinates	Alt. (m)	Habitat type
Yongin	37°06'32.08" N-127°10'49.79"E	32	Reservoir channel (upper region)
Hongsung	36°32'42.71" N-126°41'34.56"E	31	Stream shore (midstream)
Paju	37°42'54.25" N-126°41'20.49"E	8	Stream shore (downstream)

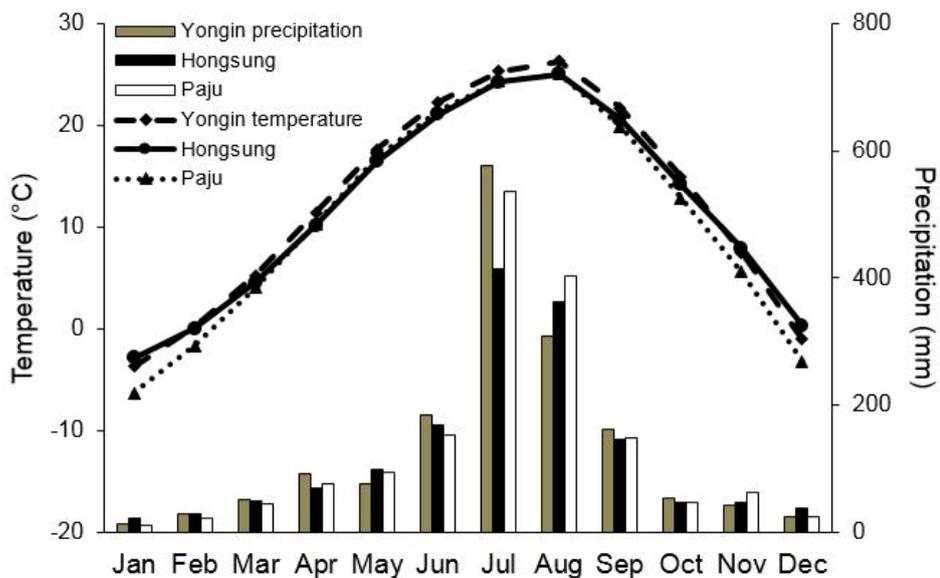


Fig. 1 Monthly mean temperature and precipitation at Yongin, Paju, and Hongsung during 2008 - 2012 (range of temperature: -18.6 ~ 37.4 °C (Yongin), -20.1 ~ 35.1 °C (Paju) and -15.1 ~ 36.0 °C (Hongsung); data from National Weather Service, 2014).

2.3 Mesocosm experiment

2.3.1 Sampling and culture of plants

Rhizomes of *P. chinense* were collected from a natural population at a waterside site in Hongseong. Unfortunately, not enough *P. chinense* were collected from the site in Hongseong because *P. chinense* is rare and I had no choice but to

buy *P. chinense*. I purchased rhizomes of *P. chinense* that was cultivated at a paddy field side in Gangneung, Korea. And then they were brought to a greenhouse in Seoul National University in April 2012. When shoots from the rhizomes had grown to about 10 cm in height in plug trays, they were transplanted into pots (11.5 cm diameter and 13.5 cm depth), with the exception of the nutrient reduction treatment samples, which were transplanted to containers (3.5 cm wide, 5.5 cm long, and 10 cm depth). One plant was transplanted to each pot or container. Each group had six replicates. The experiment was set up by considering fresh weight and shoot length of each plant obtained prior to transplantation. Treatments were initiated at 1 week after the transplant to acclimatize. Position of the pots were completely randomized and were rotated at least monthly so that all plants experienced the same environmental conditions within each treatment. Each treatment was performed for different lengths of time as follows: N-supplement treatment from June to July, nutrient reduction treatment from July to October, light intensity and soil water content treatment from June to October, and post-submergence treatment from July to October 2012. The air temperature and relative humidity in the greenhouse were in the range of 1.0 ~ 37.2 °C and 21.6 ~ 100.0 %, respectively (Fig. 2), and were measured using Hobo data logger (Part U23-001, Onset Corp., Pocasset, MA) every hour during the period of June to October 2012. The PARs of 203.8 ~ 1488.4 $\mu\text{mol m}^{-2} \text{s}^{-1}$ were recorded between 12:00 and 13:00 KST, during the same period of June to October.

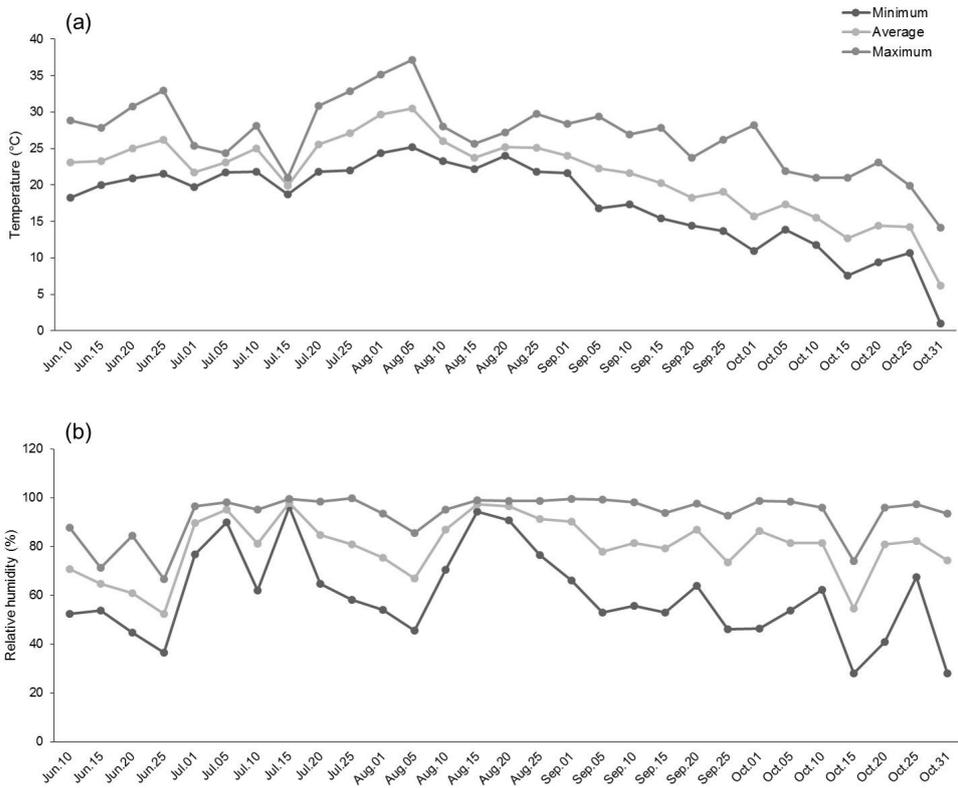


Fig. 2 Environmental conditions of the growth experiments (a) temperature, (b) relative humidity

2.3.2 Light intensity treatment

A total of 30 plants were transplanted to pots that were filled with a mixture (1:5, v/v) of potting compost soil and river-sand; the mixture contained a similar concentration of nutrients ($6.48 \text{ mg kg}^{-1} \text{ NO}_3\text{-N}$ and $7.44 \text{ mg kg}^{-1} \text{ PO}_4\text{-P}$) as that is in the habitat (Table 2). Five groups were applied: full light (FH), high light (HL), medium light (ML), low light (LL), and extreme low light (ELL). The pots except FH group were enclosed by black polyester nets designed to reduce light transmission for solar radiation penetrating through the sides of the plants respectively. The top of the shade cloth was elevated to track height growth. The mean percent PAR (mesocosm) \pm s.e. was $75.48 \pm 0.96 \%$ (FL), $52.89 \pm 1.20 \%$ (HL), $21.83 \pm 0.53 \%$ (ML), $7.01 \pm 0.33 \%$ (LL), and $2.69 \pm 0.32 \%$ (ELL), respectively; The *percent PAR (mesocosm)* = PAR of each groups / PAR of open air surrounding of greenhouse.

2.3.3 N-supplement treatment

This treatment was processed with full strength modified Hoagland's solution (Shiple and Keddy 1988), into the 4 groups of total nitrogen concentrations of 9.0 mM (full Hoagland group), 6.3 mM (N70 group), 3.6 mM (N40 group), and 0.9 mM (N10 group); only nitrogen concentrations were adjusted. A total of 24 plants were transplanted to pots filled with river-sand ($0.58 \text{ mg kg}^{-1} \text{ NO}_3\text{-N}$, $6.61 \text{ mg kg}^{-1} \text{ PO}_4\text{-P}$). I placed a pot in a container (18 cm wide, 12 cm long, and 10 cm depth) and the relevant nutrient solutions were completely renewed in the containers every 3 days. The soil of pots was saturated as the pots were submerged in the nutrient solutions to the level as close as possible to the soil surface. Soil N and P concentrations for the N10 group were slightly higher than the maximum values in their habitats (Table 2).

2.3.4 Nutrient reduction treatment

The nutrient solutions were based on the N10 group and diluted with deionized water to obtain three nitrogen concentrations: 0.3 mM (1/3 group), 0.09 mM (1/10 group), and 0.009 mM (1/100 group). A total of 18 plants were transplanted to containers (3.5 cm wide, 5.5 cm long, and 10 cm depth) which were filled with relevant nutrient solutions under hydroponics; the solutions were completely renewed every 3 days. For the 1/3 group, the soil N and P concentrations were slightly higher than the habitat mean value. In both the nitrogen addition and nutrient reduction experiments, the cover was placed over each container in order to minimize evaporation and reduce algal growth in the nutrient solution.

2.3.5 Soil water content treatment

A total of 24 plants were transplanted to pots that were filled with a mixture (1:5, v/v) of potting compost soil and river-sand; the mixture contained a similar concentration of nutrients ($6.48 \text{ mg kg}^{-1} \text{ NO}_3\text{-N}$ and $7.44 \text{ mg kg}^{-1} \text{ PO}_4\text{-P}$) as that is in the habitat. Four groups were applied: waterlogging (W), high soil water content (HW), medium soil water content (MW), and drought (D). The pots in the waterlogged group were submerged in tap water to the level as close as possible to the soil surface. In the other groups, the pots were allowed to dry to a respective designed soil water content and given tap water to each calculated capacity every day to maintain the relevant soil water content level measured using a soil moisture probe meter (WT1000N, RF sensor, Korea). I determined the amount of watering required each day by calculating according to the following equation, using linear regression analysis: $y=0.079x+1.017$ ($n=4$, $R^2 = 0.956$, $P = 0.022$), where x is the amount of watering required each day and y is the soil moisture content determined using a soil moisture probe meter. The results measured with a soil moisture probe meter were converted into the values calculated according to the following regression equation: $y=0.603x+4.286$ ($n=10$, $R^2 = 0.931$, $P < 0.001$), where x is the

soil moisture content determined using a soil moisture probe meter and y is the soil moisture content determined gravimetrically by oven drying at 105°C for ≥ 24 hours. The mean soil water content \pm s.e. before and after watering was $23.89^d \pm 0.10\%$ (W), $16.99^c \pm 0.26\%$ (HW), $11.39^b \pm 0.15\%$ (MW), and $7.65^a \pm 0.081\%$ (D), respectively ($P < 0.001$; The different superscript letters indicate significant differences among groups of means based on post hoc tests).

2.3.6 Submergence and post-submergence treatments

A total of 48 pots were filled with a mixture (1:5, v/v) of potting compost soil and river-sand, and the mixture contained a similar concentration of N and P ($1.75 \text{ mg kg}^{-1} \text{ NO}_3\text{-N}$, $11.94 \text{ mg kg}^{-1} \text{ PO}_4\text{-P}$) as that of the habitat. The submergence of both treatments started in July 2012 and their duration was 15 days. The flooding period and duration in the field were chosen for the experiments. The mean height of the initial plants was 14.0 cm and four different flooding groups were applied: (1) control (C) – no flooding; (2) partial submergence (PS) – water level maintained at 8.5 cm above the soil surface; (3) complete submergence (CS) – plants fully submerged under 40 cm above the soil; and (4) shaded/complete submergence (SCS) – plants fully submerged and covered with black polyester nets. The shade cloth was used to mimic low light environments typically found in turbid floodwater areas. For SCS treatment, the light intensity was determined by results from testing as follows. I put habitat soil (40 g), which was silt loam soil texture, in 1L mess cylinder and filled the mess cylinder with water to 1L volume. And then I repeated shaking up and down 30 times for 1 minute and measured PARs in the solution every minute. The submergence of both treatments was conducted in outdoor tanks (83 cm wide, 166 cm long, and 53 cm depth). Within the tanks of each group, pots were allocated randomly and located at least 10 cm from the walls. The tanks were filled with tap water, which was replaced with flood water twice a week (range of water temperature: $19.2 \sim 35.9 \text{ }^\circ\text{C}$ (PS), $19.8 \sim 35.4 \text{ }^\circ\text{C}$ (CS) and $20.0 \sim 31.0 \text{ }^\circ\text{C}$ (SCS); DO: $20.2 \sim 30.5 \text{ mg kg}^{-1}$ (PS), $19.7 \sim$

30.7 mg kg⁻¹ (CS) and 18.4 ~ 28.8 mg kg⁻¹ (SCS); and conductivity: 108.9 ~ 167.3 μS cm⁻¹ (PS), 117.4 ~ 168.1 μS cm⁻¹ (CS) and 122 ~ 172.2 μS cm⁻¹ (SCS)). The water temperature was measured using TidbiT v2 temperature logger (Part UTBI-001, Onset Corp., Pocasset, MA) every hour. And DO and conductivity of this water was measured with a DO meter (Orion 3 Star Portable DO meter, Thermo Fisher Scientific) and with a conductivity meter (Checkmate Model 311, Corning, New York, USA), respectively. The PARs measured at the plant level were 212.0 ~ 1721.6 μmol m⁻² s⁻¹ in the PS, 171.92 ~ 1688.8 μmol m⁻² s⁻¹ in the CS, and 8.97 ~ 93.36 μmol m⁻² s⁻¹ in the SCS group. All conditions except water temperature were measured between 12:00 and 13:00 KST. After 15 days of submergence, we harvested half of these plants in each group (submergence treatment); the remaining plants were transferred back to the control conditions and recovery was monitored until October (post-submergence treatment).

2.3.7 Data collection

During the experimental period, the height, amount of leaf chlorophyll, and anthesis were monitored twice a week. Leaf chlorophyll in fully expanded young leaves (30 samples per individual) was measured using a chlorophyll meter (SPAD-502 Plus, Konica Minolta, Japan). Plant survival was determined based on plant appearance, and plants with any green turgid leaves were assigned as viable. At harvest, the roots were carefully washed free of soil substrate, and plants were separated into leaves, stems, roots, rhizomes, fruit skins, seeds, and buds. The weight of each organ was measured after drying to constant weights at 80 °C. Another 30 plants were harvested at the beginning of the experiment in order to determine the initial plant biomass. The leaf area was measured using a Portable Leaf Area Meter (LI-3000C, LI-COR Bioscience, Lincoln, Nebraska, USA). The total weight and number of the seeds sown in a weighing dish were used to determine the weight of a single seed, which was used to estimate the total number of seeds. Seeing the images taken from a digital microscope camera (EGVM-13M,

EG-Tech, Korea), I counted the seeds sown in the weighting dish. The subsamples of the leaf and stem were ground with a ball mill. And then the total nitrogen (T-N) was determined using an Elemental Analyzer (Flash EA 1112, Thermo Scientific, Waltham, Massachusetts, USA) and the total phosphate (T-P) was analyzed using Inductively Coupled Plasma Mass Spectrometer (Varian 820-MS, Varian, Australia) at the National Center for Inter-University Research Facilities, Seoul National University.

2.3.8 Data analyses

Variables were calculated from the following equations: height per total plant mass = height / total plant dry mass (cm g^{-1}); specific leaf area = leaf area / leaf dry mass ($\text{cm}^2 \text{g}^{-1}$); root mass fraction = root dry mass / total plant dry mass (g g^{-1}); seed mass fraction = seed dry mass / total plant dry mass (g g^{-1}); rhizome mass fraction = rhizome dry mass / total plant dry mass (g g^{-1}); Relative growth rates (RGR) were calculated for total biomass increase as $\text{RGR} = [\ln(\text{final total dry weight}) - \ln(\text{initial total dry weight})] / \text{days}$; N:P ratio = N concentration of leaf or stem / P concentration of leaf or stem; and Reproductive allocation = sexual reproductive organ (buds, flowers and fruits) dry mass / total plant dry mass $\times 100$ (g g^{-1}).

2.4 Statistical analyses

One-way analysis of variance (ANOVA) and Duncan's multiple range test were performed with a significance level of 5%. ANOVA assumptions were checked, and data was \log_{10} or square-root transformed if normal distribution and/or homogeneity of the variances was not achieved. When normal distribution and/or homogeneity of the transformed variances was not achieved, the data was subjected to the Kruskal–Wallis nonparametric test, followed by the Games–Howell nonparametric multiple comparison test. The statistical analyses were performed using PASW statistics 18 version 18.0.0 (SPSS Inc., Chicago, IL, USA).

In a field survey, to identify significant predictors of *P. chinense* habitat preference, I first conducted a Canonical Correspondence Analysis (CCA) by using Canoco 4.5 for Windows (ter Braak and Smilauer 2002). I conducted CCA regarding vegetation variables because the variables except vegetation variables were not investigated at all quadrats. The most important environmental variables were identified by forward selection. Only factors statistically significant at $P < 0.05$ confidence level were selected for the final analysis (Table 5). The statistical significance of Axes 1 and 2 was tested by using a Monte Carlo permutation test with 999 permutations under the full model. I also conducted univariate analyses in the field survey because univariate analyses can identify factors potentially associated with habitat preference (Table 4). All results are presented as non-transformed mean \pm s.e.

3. Results

3.1 Field survey

The distribution range of *P. chinense* indicates its realized niche (Table 2). Pure stands of one year old *P. chinense* and communities of annual and biennial plants with it have low degree of succession. *P. chinense* are largely found in these sites, which are the reset point for establishing new pioneer species after forming open space by disturbance. A small amount of *P. chinense* was distributed in communities of large perennials and shrubs to maintain the succession under progress (Table 2). Likewise, quadrates including many *P. chinense* and pure stands of *P. chinense* were open space with 100 % of percent PAR (field), and I did not find *P. chinense* at low percent PAR (field) quadrates (Table 2). In *P. chinense* habitats, the contents of soil organic matter, NO₃-N, and PO₄-P were relatively low, the range of soil pH was wide from acidic to basic, and the sand content was high in most sites (Table 2). Especially, sandy soils including gravel were found in Yongin. The concentrations of gravel in the 3 samples were relatively high (Table

3). There was a bigger stone placed on the sample that was dug up from the site (23.1 ± 6.2 cm long, 19.6 ± 5.0 cm wide, and 9.4 ± 5.8 cm height). *P. chinense* typically occurred at a relatively low water depth or in waterside locations of 7 to -9 cm and was found in sites with a wide range of water content from waterlogged soils to dry soils (Table 2). Most habitats were water-level-fluctuation zones that seasonally flooded in the rainy season of July or September. When the quadrats were submerged under flood water in July, the depth of the water was measured about 1m and the current velocity was $52 \sim 72$ cm s⁻¹. However I observed that *P. chinense* regenerated from stems and rhizomes even though some *P. chinense* stems fell down after the floods.

Table 2 Range of variables (mean \pm s.e.) at 38 quadrats where *P. chinense* occurred.

Vegetation variables	
Degree of succession	9.02 ~ 1031 (241 \pm 36)
Shannon-Wiener H'	0.07 ~ 2.20 (1.28 \pm 0.10)
Importance value of annual and biennial	0.01 ~ 0.81 (0.27 \pm 0.04)
Mean height of plant community (cm)	7.33 ~ 130 (47.57 \pm 5.51)
Total cover of plant community (%)	13.00 ~ 100 (74.92 \pm 3.83)
Soil variables (12 samples)	
Organic matter (%)	0.89 ~ 4.38 (2.40 \pm 0.20)
Soil texture	sand(24), sandy loam(4), silt loam(10)
Sand (%)	13.85 ~ 94.98 (72.03 \pm 4.69)
Silt (%)	1.25 ~ 77.28 (21.86 \pm 4.50)
Clay (%)	3.76 ~ 8.87 (6.11 \pm 0.31)
Fresh soil moisture (%)	7.96*, 13.70 ~ 39.80 (25.31 \pm 2.27)
pH	5.80 ~ 8.72 (7.06 \pm 0.15)
NO ₃ -N (mg kg ⁻¹)	0.04 ~ 12.61 (2.74 \pm 0.64)
PO ₄ -P (mg kg ⁻¹)	0.75 ~ 28.42 (11.27 \pm 1.46)
Water variables (4 samples)	
pH	6.63 ~ 7.09 (6.88 \pm 0.10)
Turbidity (NTU)	7.16 ~ 22.90 (12.89 \pm 2.98)
NO ₃ -N (mg L ⁻¹)	0.00019 ~ 4.16 (1.18 \pm 0.87)
PO ₄ -P (mg L ⁻¹)	0.019 ~ 0.43 (0.15 \pm 0.08)
Percent PAR (field) (%) ¹	11.94 ~ 100 (69.27 \pm 4.00)
Water depth (cm) ²	-9.00 ~ 7.00 (-0.90 \pm 0.41)

* Extreme dry case.

¹ Measured 58 samples, recorded 0.79 ~ 13.98 (7.84 \pm 1.47) % at 2 quadrats absent (adjacent to) of *P. chinense* shoots with large size plant species (10 samples).

² Measured at 23 quadrats (69 samples)

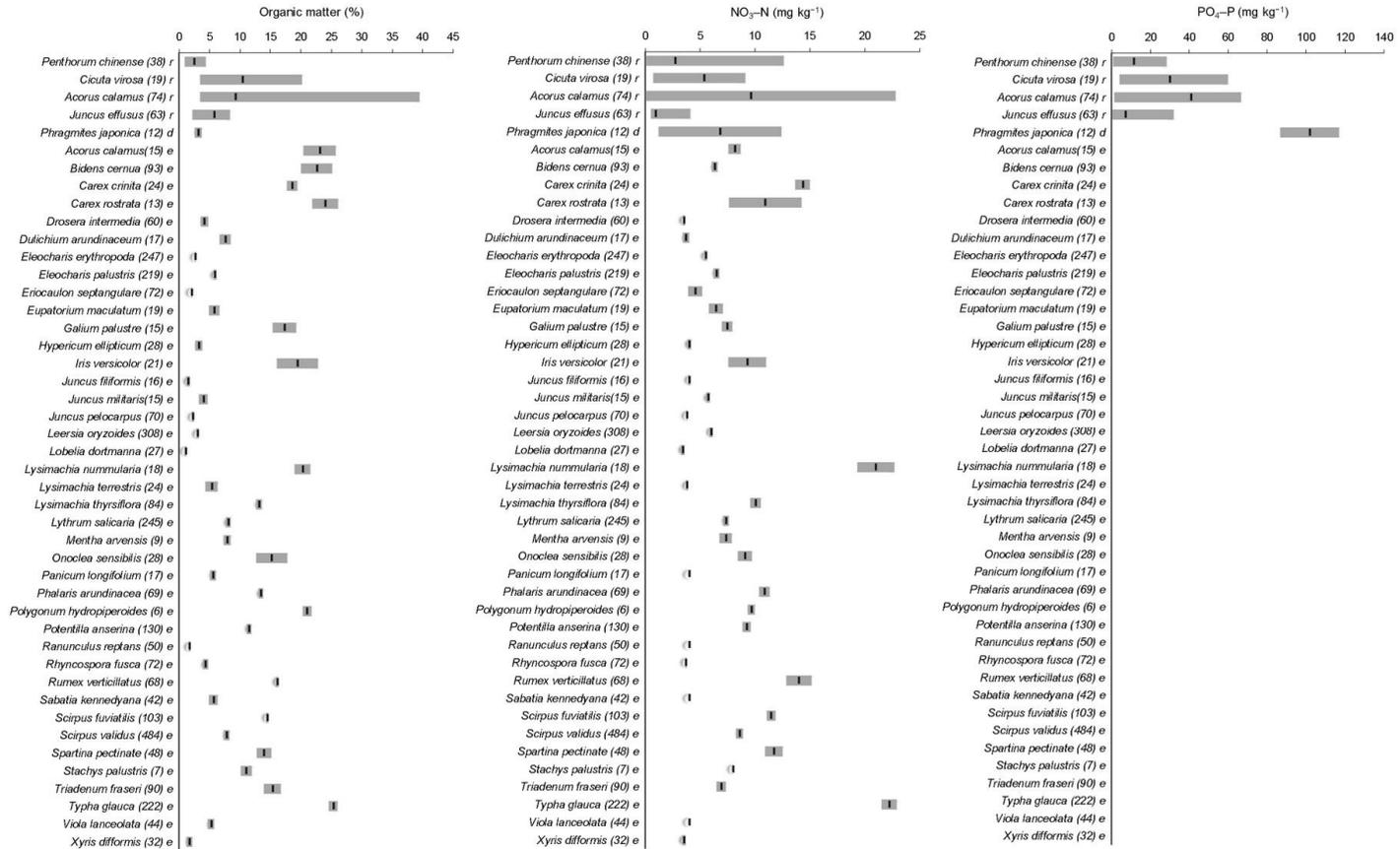


Fig. 3 Range of values (gray bars) and means (black lines) of organic matter content, NO₃-N and PO₄-P concentrations of wetland plant species (number of quadrats given after species names; range of values indicates that r is values from minimum to maximum in total distributional range, d is standard deviation and e is standard error; data from: Gaudet & Keddy 1995; Jeon et al. 2010; Yoon et al. 2011; Hong et al. 2012; Shin et al. 2013).

Table 3 Soil profile fragments concentration (weight %) for 3 samples of a *P. chinense* habitat in Yongjin.

Fragments size (mm)	Sample 1	Sample 2	Sample 3
2 and below (soil)*	25.3	21.0	27.6
2 - 6	8.8	6.9	6.9
6 - 10	3.6	2.3	1.9
10 - 20	10.6	8.5	4.6
20 - 40	5.4	9.8	3.2
40 - 50	4.9	7.9	7.2
50 - 80	18.4	14.4	5.2
80 and above (including gravel)	22.9	29.1	43.3

*Soil texture (mean \pm s.e.): sand (81.70 ± 1.69 %), silt (11.04 ± 1.42 %) and clay (7.25 ± 0.79 %).

I classified and analyzed all quadrats to understand the habitat preference of *P. chinense*. Groups 1 and 3 with a high importance value of *P. chinense* had a lower mean height of plant community, lower degree of succession, more percent PAR (field), lower organic matter content, more sand, and less silt than Group 2 which had a low importance value of *P. chinense* (Table 4). Group 1 had the highest importance value of annual and biennial plants and the lowest total cover of plant community; however, for Shannon-Wiener H' there was no significant difference between Groups 1 and 2 (Table 4). Group 3 on the other hand was a pure stand of *P. chinense* and had the lowest Shannon-Wiener H', low importance value of annual and biennial plants, and high total cover of plant community (Table 4). The CCA biplot supports the grouping method. It showed that Axis 1 was predominantly community mean height gradient (Fig. 3). Thus, Group 1 and 3, which had a high *P. chinense* importance value, were situated toward the right of Axis 1, and separated from Group 2 by their smaller community mean height. The dominant environmental variable correlated with Axis 2 was Shannon-Wiener H'

and other factors associated with Axis 2 were annual, biennial importance value and community cover (Fig. 3). As Group 1 was situated toward the top of Axis 2, Shannon-Wiener H' and annual, biennial importance value were showed higher tendency and community cover was showed lower tendency than the others, although pure stands, Group 3, indicated opposite tendency at Group 1 because the communities consisted of mostly *P. chinense*. Axes 1 and 2 accounted for 40.0% and 25.8% of the explained variance, respectively (Table 5), and both axes were significant at $P < 0.005$ (Monte Carlo test).

Table 4 Results of ANOVA on vegetation and soil variables of *P. chinense* habitat groups.

	Group 1	Group 2	Group 3
Importance value of <i>Penthorum chinense</i>	0.31 ± 0.05 ^b	0.036 ± 0.008 ^a	0.85 ± 0.03 ^c
Vegetation variables			
Degree of succession	169 ± 32 ^b	382 ± 46 ^c	46.3 ± 4.7 ^a
Shannon-Wiener H'	1.60 ± 0.11 ^b	1.32 ± 0.12 ^b	0.37 ± 0.09 ^a
Importance value of annual and biennial	0.51 ± 0.07 ^b	0.15 ± 0.02 ^a	0.11 ± 0.02 ^a
Mean height of plant community (cm)	20.04 ± 2.64 ^a	86.07 ± 7.64 ^b	28.24 ± 5.58 ^a
Total cover of plant community (%)	54.08 ± 7.40 ^a	83.13 ± 3.40 ^b	90.50 ± 3.99 ^b
Percent PAR (field) (%) [*]	100 ^b	41.22 ± 4.05 ^a	100 ^b
Soil variables			
Organic matter (%)	1.66 ± 0.17 ^b	3.48 ± 0.16 ^c	1.06 ± 0.06 ^a
Sand (%)	86.79 ± 1.68 ^b	56.87 ± 6.70 ^a	92.47 ± 0.75 ^c
Silt (%)	7.13 ± 1.25 ^b	36.42 ± 6.47 ^c	2.67 ± 0.37 ^a
Clay (%)	6.08 ± 0.60 ^{ab}	6.71 ± 0.38 ^b	4.87 ± 0.44 ^a
Fresh soil moisture (%)	20.18 ± 1.42 ^a	31.62 ± 0.95 ^b	18.66 ± 1.37 ^a
pH	7.04 ± 0.18 ^{ab}	7.32 ± 0.22 ^b	6.41 ± 0.20 ^a
NO ₃ -N (mg kg ⁻¹)	1.37 ± 0.64 ^a	3.41 ± 0.97 ^a	1.63 ± 0.64 ^a
PO ₄ -P (mg kg ⁻¹)	12.49 ± 2.58 ^b	5.24 ± 0.68 ^a	23.23 ± 1.13 ^c

Values are mean ± s.e. The different superscript letters within the rows indicate the significant differences ($P < 0.05$) among groups based on post hoc tests; Group 1: quadrates including many *P. chinense* (n=12), Group 2: quadrates including a few *P. chinense* or absent (adjacent to) of *P. chinense* (n=23) and Group 3: pure stands of *P. chinense* (n=8).

^{*} Measured 58 samples, recorded 0.79 ~ 13.98 (7.84 ± 1.47) % at 2 quadrats absent (adjacent to) of *P. chinense* shoots with large size plant species (10 samples).

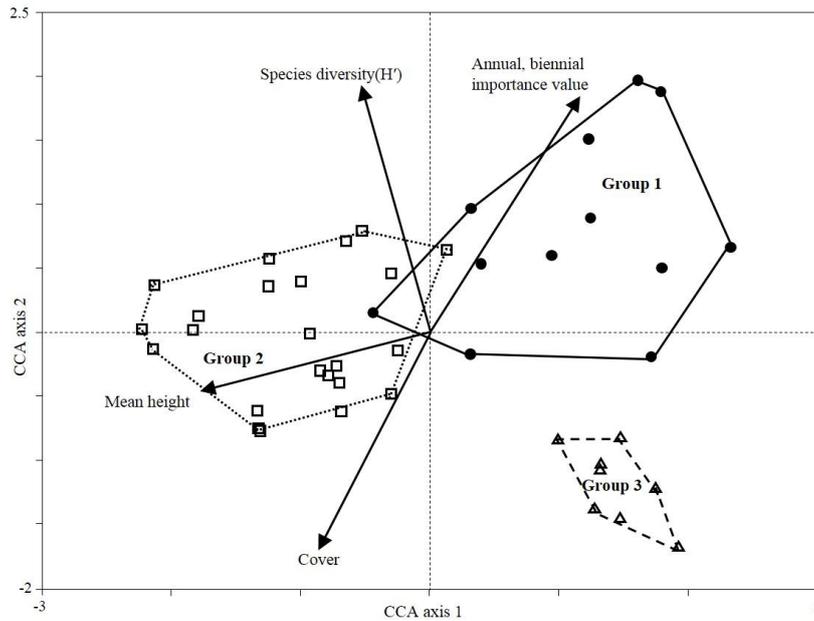


Fig. 4 Canonical Correspondence Analysis (CCA) pertaining to vegetation variables for habitat of *P. chinense*.

Table 5 Summary statistics of the CCA pertaining to vegetation variables for habitat of *P. chinense*.

Axes	1	2	3	4
Eigen values	0.631	0.406	0.351	0.188
Species-environment correlations	0.915	0.920	0.775	0.611
Cumulative percentage variance				
of species data	11.4	18.7	25.1	28.5
of species-environment relation	40.0	65.8	88.0	100.0
Inter-set correlations with axes				
Community mean height	-0.7301	-0.1834	-0.3007	0.2544
Shannon-Wiener H'	-0.2213	0.7791	0.3042	-0.1625
Annual, biennial importance value	0.4698	0.7407	-0.1915	-0.1014
Community cover	-0.3470	-0.6711	-0.2756	-0.2718

3.2 Mesocosm experiment

All the individual plants survived, grew, and reproduced both asexually and sexually under all treatments except ELL (Fig. 4a ~ f). In addition, the seed number and final germination percentage of *P. chinense* did not drastically decrease, even during severe stress except LL in our experiment (Table 6). The results show how *P. chinense* has a large fundamental niche of the soil nutrient and water content. The response to stresses demonstrates which ecological characteristics are selected from *P. chinense* under various stress conditions and whether or not *P. chinense* is able to tolerate a variety of types and intensity of stress, based on previous studies. At harvest date, *P. chinense* was a small stature (height: 82.17 ± 5.08 cm, total plant dry weight: 16.72 ± 0.77 g, n=6) and had short rhizomes (length: 4.18 ± 0.39 cm, min 0.1 cm, max 15 cm, n=85) and rhizome expansion was slow (total rhizome dry weight: 0.93 ± 0.07 g y⁻¹, total rhizome length: 59.17 ± 5.37 cm y⁻¹, n=6) under the environmental conditions of control treatment.

3.2.1 Nutrient reduction treatment

The total plant, seed, and rhizome dry mass did not significantly differ among the 1/3, 1/10 and 1/100 groups (Fig. 4a). However, the root mass fraction of the 1/10 and 1/100 groups was higher than that of the 1/3 group (Table 6). The N concentration of the stem did not differ significantly among the 1/3, 1/10 and 1/100 groups (Table 6). The total plant dry mass, rhizome dry mass and N concentration of the stem had the highest value in N10 group (Table 6, Fig. 4a).

3.2.2 N supply treatment

The total plant dry mass had the lowest value in the N10 group and the species reached much better growth when N was added (Fig. 4b). In groups N10 to N70, the total plant dry mass increased, but that in the N100 group did not significantly differ from that in the N70 group.

3.2.3 Soil water content treatment

The total plant and seed dry mass had the highest value in HW (Fig. 4c). D showed the highest mean of root mass fraction, chlorophyll, and N concentration of stem (Table 6). In W, the root grew more than the initial plants, and there was no significant difference at both the root dry mass and N concentration of the stem compared to HW (Table 6).

3.2.4 Submergence treatment

Aquatic adventitious roots were emerged at the submerged parts of the inundated groups. SCS, CS, and PS were all greater than C in height per total plant mass and specific leaf area during the 15 days of submergence (Table 6). However, SCS, CS, and PS all grew in height compared to their initial state, while PS was taller than C, and SCS and CS were shorter than C (Table 6). The total plant dry mass at SCS and CS did not significantly differ from its initial condition (Fig. 4d).

3.2.5 Post-submergence treatment

When the *P. chinense* plants had recovered after 15 days of partial submergence (PS), the time to flowering was accelerated and the seed mass fraction was greater than C (Table 6). On the other hand, after 15 days of complete submergence (SCS, CS), the time to flowering was delayed and the rhizome mass fraction was greater than C (Table 6).

3.2.6 Light intensity treatment

All the plants of ELL group died in July, but all the individual plants of the different groups survived, grew, and reproduced both asexually and sexually (Fig. 4f). The plants of LL group had very low seed number (3.01 ± 1.19 %, min 0 %, max 8.05 % of the FL seed number) even if the final germination percentage of the plants was high. The percent PARs (mesocosm) of LL and ELL concurred with the percent PARs (field) of quadrats absent (adjacent to) of *P. chinense* shoots with large size plant species.

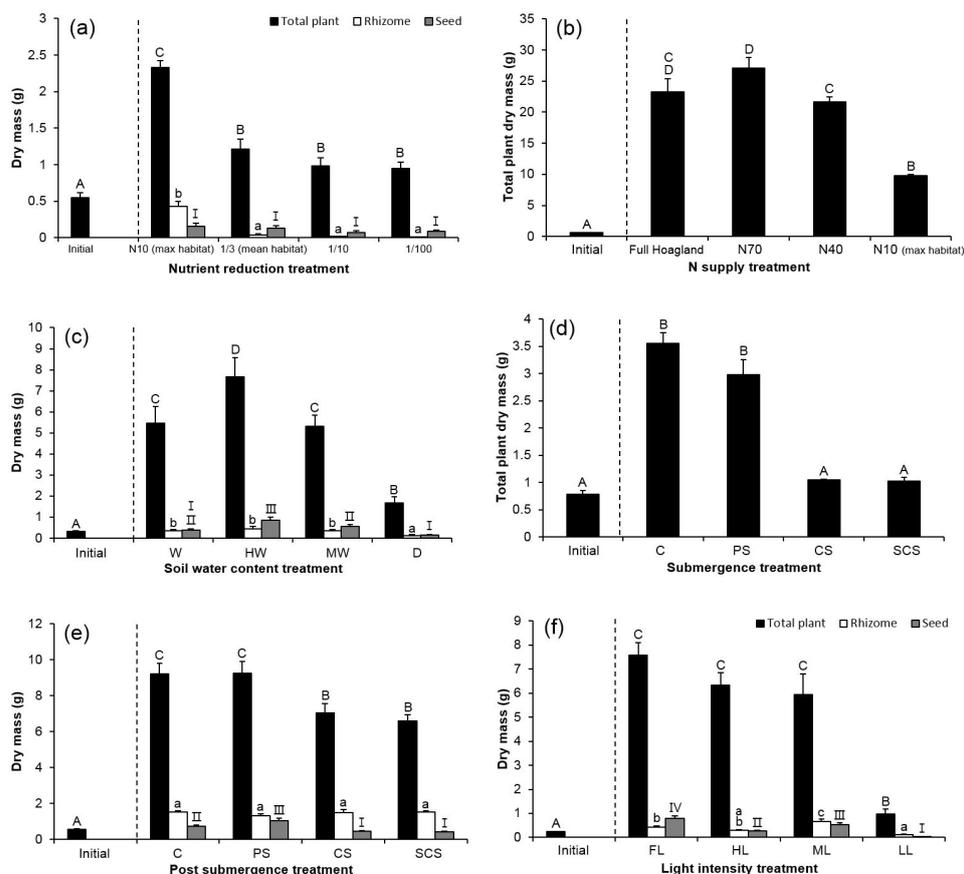


Fig. 5 Total plant, rhizome and seed dry mass (mean \pm s.e. by plot) of *P. chinense* plants subjected to (a) nutrient reduction treatment, (b) N supply treatment, (c) soil water content treatment and (d) submergence treatment (e) post submergence treatment (f) light intensity treatment. The different letters indicate the significant differences ($P < 0.05$) among groups based on post hoc tests; FL: full light, HL: high light, ML: medium light, LL: low light, W: waterlogging, HW: high soil water content, MW: medium soil water content, D: drought, C: control, PS: partial submergence, CS: complete submergence, SCS: shaded complete submergence.

Table 6 Summary of variances associated with tolerance to environmental conditions of *P. chinense*.

Nutrient reduction treatment	N10 (maximum habitat)	1/3 (mean habitat)	1/10	1/100
Seed number (10^4 no.)	1.72 ± 0.45^a	1.57 ± 0.37^a	0.78 ± 0.28^a	0.99 ± 0.13^a
Final germination percentage (%)	72.66 ± 13.72^a	72.24 ± 15.25^a	92.25 ± 1.69^a	92.21 ± 3.14^a
Root mass fraction (g g^{-1})	0.38 ± 0.019^a	0.39 ± 0.010^a	0.45 ± 0.013^b	0.46 ± 0.0084^b
N concentration of stem (mg N g^{-1})	4.83 ± 0.15^b	3.26 ± 0.37^a	3.09 ± 0.43^a	2.30 ± 0.080^a
Soil water content treatment	W	HW	MW	D
Seed number (10^4 no.)	3.19 ± 0.60^b	9.03 ± 1.71^c	5.80 ± 0.87^{bc}	1.38 ± 0.46^a
Final germination percentage (%)	96.14 ± 0.76^a	98.74 ± 0.50^a	96.34 ± 1.89^a	94.16 ± 2.17^a
Root mass fraction (g g^{-1})	0.38 ± 0.03^a	0.35 ± 0.02^a	0.37 ± 0.01^a	0.42 ± 0.03^b
SCMR (SPAD chlorophyll meter readings)	40.78 ± 0.56^a	39.95 ± 0.23^a	40.53 ± 0.29^a	48.27 ± 0.97^b
N concentration of stem (mg N g^{-1})	1.87 ± 0.09^a	2.52 ± 0.26^a	1.97 ± 0.12^a	4.98 ± 0.58^b
Root dry mass (g) ¹	2.14 ± 0.39^{bc}	2.57 ± 0.18^c	1.95 ± 0.21^c	0.70 ± 0.13^b
Submergence treatment	C	PS	CS	SCS
Height per total plant mass (cm g^{-1})	7.47 ± 0.33^a	10.04 ± 0.44^b	19.98 ± 0.76^c	22.39 ± 1.34^c
Specific leaf area ($\text{cm}^2 \text{g}^{-1}$)	219 ± 4^a	248 ± 9^b	327 ± 14^c	339 ± 8^c
Height (cm) ²	26.30 ± 0.70^c	29.32 ± 1.39^d	20.95 ± 0.71^b	22.82 ± 0.78^b
Total plant dry mass (g) ³	3.56 ± 0.19^b	2.98 ± 0.28^b	1.05 ± 0.02^a	1.03 ± 0.06^a

Table 6 Continued.

Post submergence treatment	C	PS	CS	SCS
Seed number (10^4 no.)	7.98 ± 0.67^b	12.04 ± 1.42^c	5.11 ± 0.23^a	4.58 ± 0.41^a
Final germination percentage (%)	87.49 ± 6.75^a	94.53 ± 2.71^a	95.88 ± 1.26^a	96.58 ± 0.68^a
Time to flowering (day)	55.67 ± 0.84^b	48.33 ± 1.91^a	60.33 ± 0.67^c	62.50 ± 1.50^c
Seed mass fraction (g g^{-1})	0.080 ± 0.005^a	0.112 ± 0.009^b	0.065 ± 0.005^a	0.063 ± 0.005^a
Rhizome mass fraction (g g^{-1})	0.17 ± 0.007^a	0.14 ± 0.011^a	0.20 ± 0.014^b	0.23 ± 0.008^b
Light intensity treatment	FL	HL	ML	LL
Seed number (10^4 no.)	6.82 ± 1.05^c	3.52 ± 0.48^b	5.03 ± 0.75^{bc}	0.21 ± 0.08^a
Final germination percentage (%)	98.17 ± 0.63^a	99.00 ± 0.16^a	98.51 ± 0.51^a	98.73 ± 0.83^a

Values are mean \pm s.e. The different superscript letters within the rows indicate significant differences among groups of means based on post hoc tests; W, waterlogging; HW, high soil water content; MW, medium soil water content; D, drought; C, control; PS, partial submergence; CS, complete submergence; SCS, shaded complete submergence; FL, full light; HL, high light; ML, medium light; LL, low light.

¹ initial plants: 0.14 ± 0.007^a , ² initial plants: 14.02 ± 0.64^a , ³ initial plants: 0.78 ± 0.08^a .

4. Discussion

The research reveals that *P. chinense* has a narrow realized niche that requires oligotrophy and disturbance, while the fundamental niche of the soil nutrients and water content appears to be large. In addition, the species has a variety of tolerant traits to nutrient deficit, drought, waterlogging, and submergence for 15 days. The restricted distribution of *P. chinense* to peripheral habitats might be a strategy to reduce competition for light, similar to other rare plant species, and *P. chinense* has the strategies to persist in the habitat with alternate occurrences of flooding and drought.

4.1 Realized niche

The realized niche of *P. chinense* is characterized by a relatively low degree of succession, high percent PAR (field), low content of soil organic matter, NO₃-N, and PO₄-P, much sand among the soil texture classes, and low water depth or watersides with a wide range of water content from waterlogged soils to dry soils of the water-level-fluctuation zone. In a previous study, the contents of soil organic matter and PO₄-P were within our data range, but the soil texture range was wider than our range. However, sandy loam and sand with a higher sand content predominated, similar to our data (Shin 2011), and the average water depth similar to our result (Kang et al. 2003). It is suggested that *P. chinense* occurs in a narrow realized niche characterized by an oligotrophic sandy riparian zone, and the species is a pioneer species recolonized at the wetland's reset point by disturbance. *P. chinense* also inhabits the small gaps formed by the less dense canopy of large plants such as interstitial perennials (Boutin and Keddy 1993).

The habitat preference of *P. chinense* can be summarized as: relatively low mean height of plant community, total cover of plant community, degree of succession, organic matter and silt content, and relatively high importance value of annual and biennial, percent PAR (field) and sand content. These results concur with previous works in which the main habitats of *P. chinense* were dominated by

annual plant communities, had relatively low mean height of plant community, total cover of plant community, degree of succession and humus layer cover, had relatively high species number (Kang et al. 2003), and the species was mostly distributed in locations with high light intensity (Ohkuro et al. 2003). It is considered that *P. chinense* tends to be more vigorous in open spaces formed by flooding, and is extirpated with increased canopy shading by large and rapidly growing perennials through ecological succession (Kang et al. 2003).

4.2 Responses to stresses

4.2.1 Responses to nutrient deficit

Root mass fraction of *P. chinense* showed a higher value for groups from 1/10 to 1/100 than the 1/3 group (mean habitat) and the higher increase in allocation to roots in oligotrophic soils represents an adaptive plastic response (Useche & Shipley 2010). According to the theory of a ‘functional equilibrium’, plants shift allocation towards roots at a low level of below-ground resources, such as nutrients and water, and these shifts could be seen as adaptive because they enable the plant to capture more of those resources that most strongly limit plant growth (Brouwer 1963). *P. chinense* maintained nitrogen concentrations under N-depleted conditions, unlike fast-growing species; this is also known to take place in *Festuca ovina*, which is slow-growing, and is characteristic of unproductive grasslands (Kachi and Rorison 1990). Moreover, *P. chinense* grows very slowly under natural conditions (Pan 1992) and showed low relative growth rate (RGR) ($0.057 \pm 0.001 \text{ g g}^{-1} \text{ d}^{-1}$, in Full-strength Hoagland’s solution, n=6). The slow-growing species show smaller reductions in RGR and are more resistant under frequent disturbance due to high-density tissues versus fast-growing species when facing a decrease in nitrogen availability. This could be expected to augment the survival probability of slow-growing species in infertile and frequently disturbed habitats (Useche & Shipley 2010). Thereby, the slowly growing characteristic of *P. chinense* seems to increase its abundance in these habitats.

4.2.2 Responses to water deficit

Allocation to the root system would be expected to be increased in response to water deficit in drought-adapted species (Couso & Fernández 2012). Because *P. chinense* had a plastic trait with increased root mass fraction at D, the species might be drought-adapted species. Furthermore, *P. chinense* showed the highest SCMR (SPAD chlorophyll meter readings) for D. The result indicates that the species has a trait of drought tolerance. Because there is a significantly positive correlation between SCMR and TE (transpiration efficiency is defined as the biomass produced per unit of water transpired), and high TE has been widely perceived as a useful trait for drought tolerance (Sheshshayee et al. 2006). *P. chinense* was increased in N concentration during D, which is one of the traits of drought tolerant species. Previous studies showed that water deficit treatments significantly reduced the concentration of nitrogen, compared with the control treatment, whereas in drought tolerant species the concentration of nitrogen increased, in contrast to other sensitive species (Aroca 2012). Also, a higher N concentration of the stem probably contributes to an adjustment of the cell wall elasticity. The marked increase of N content in the stem (specifically the stele) during drought could suggest that the stele is a region of protein insolubilization and such insolubilization of cell wall proteins is considered to contribute to the adjustment of cell wall elasticity, despite the water loss (Pinheiro et al. 2001).

4.2.3 Responses to waterlogging

In waterlogged soils, *P. chinense* roots grew compared to the initial state and there was no significant difference at root dry mass compared to HW. Roots often respond to waterlogging by reducing growth or even by completely ceasing growth (Malik et al. 2002). Also, waterlogging causes a significant decline in the uptake of N, P, K, Mg, and Ca compared to freely drained controls (Smethurst et al. 2005). On the other hand, Tarekegne et al. (2000) recorded a significantly reduced

nutrient uptake in waterlogging-sensitive wheat genotypes compared to more tolerant genotypes. Therefore, minimal hindrance of root growth and nitrogen concentration means that *P. chinense* is a tolerant species in environments subject to waterlogging.

4.2.4 Responses to submergence

It is considered that *P. chinense* uses the Low Oxygen Escape Syndrome (LOES) strategy. SCS, CS, and PS were all larger in height per total plant mass than C during the 15 days of submergence, indicating that the species invests more allocation to shoot extension in SCS, CS, and PS. Shoot emergence is highly beneficial for plants in flooded environments, due to the enhanced exchange of gases and the re-start of aerial photosynthesis (Colmer & Voesenek 2009). In addition, SCS, CS, and PS all had leaves with specific leaf areas that were greater than that of C. This trait reduces the diffusion resistance to gases and thus raises the rates of CO₂ entry for underwater photosynthesis and inward O₂ diffusion for respiration. In many cases, the shoots of plants with a LOES not only elongate, but also produce new leaves with a higher specific leaf area when submerged. This escape response is prevalent in plants that inhabit environments characterized by long and shallow floods (Mommer & Visser 2005). Therefore, it is considered that *P. chinense* uses the LOES strategy and inhabits environments characterized by prolonged and shallow floods (Colmer & Voesenek 2009).

Unlike the increased height per total plant mass of SCS, CS, and PS, PS was only taller than C, while SCS and CS were shorter than C. An observed plastic response may be the result of both the passive plasticity due to resource limitation, and the active plasticity as a consequence of changes in allocation (Kleunen & Fischer 2005). The observed plastic response in height for SCS and CS was lower than that for C, which is considered because inhibition of height extension by resource limitation is greater than facilitation of height extension by active plasticity under water. In addition, little biomass accumulation occurred for SCS

and CS, as also reported in submerged *A. philoxeroides* plants that use the LOES strategy (Luo et al. 2011). This may have contributed to the carbohydrate depletion in the submerged plants of *P. chinense*. Although it is known that shoot elongation provides benefits by restoring contact with the air above the floodwater, it has also been suggested that such elongation may generate expenses, as carbohydrates and energy are needed for cell division and elongation (Chen et al. 2011). This may eventually cause plant death when energy reserves are depleted before reaching the water surface (Das et al. 2005). Therefore, if *P. chinense* cannot escape from a completely submerged condition for a long period of time, it may not survive due to the cost incurred. For this reason, *P. chinense* might never have been found in stagnant deep.

4.2.5 Responses to submergence-recovery

Drawdowns affect aquatic plants both directly, by exposing them to aerial conditions, and indirectly through the modification of substrate properties (Bornette and Puijalon 2011). The time to flowering was accelerated and the seed mass fraction was greater than C when the recovery was done after 15 days of submergence in PS. This may promote a higher probability of regenerating new individuals in waterlogged systems, where physical and metabolic stresses may lower germination success and the establishment of seedlings (Mony et al. 2010). On the other hand, the rhizome mass fraction of plants recovered after 15 days submergence for SCS and CS was greater than that for C, and this trait can be found in flood-tolerant species. In clonal plants, rhizomes have two major roles in vegetative propagation: resource storage and space colonization (Kroons & Hutchings 1995). In flood-tolerant species, maintaining long rhizomes should contribute to plant survival and propagation while being inundated through the storage of carbohydrates and placement of ramets after the inundation period (Mony et al. 2010). Therefore, *P. chinense* might have the ability of resilience after a flooding.

4.3 Fundamental niche

I have shown that the results of this transplantation experiment showed successful survival, growth, and reproduction of all individuals in all treatments of soil nutrients and water contents, indicating that the fundamental niche on soil nutrients and water contents of *P. chinense* appears to be large, in contrast to its narrow realized niche.

Based on the results obtained of the fundamental niche on light intensity, soil nutrient content and realized niche of *P. chinense*, the species might be a weak competitor, as described by the centrifugal organization model (Wisheu and Keddy 1992). According to this model, weak competitors possess a large fundamental niche, reaching from productive and fertile habitats to more stressful and/or disturbed habitats. However, weak competitors will be competitively eliminated by large and rapidly growing species capable of surviving in areas that are richer in nutrients, because weak competitors are characterized by low growth rates and small stature. Weak competitors should thus be restricted to the low-productive end of their fundamental niche, i.e. to peripheral habitats, in which strong competitors are physiologically not able to maintain survival (Wisheu and Keddy 1992). When I added more nitrogen to *P. chinense* than the N10 group, with the absence of any competition, the plants grew larger in more fertile soil where the species does not occur through actual field distribution, suggesting the presence of an inclusive niche with the nitrogen content (Wisheu and Keddy 1992). If no competition occurs, the fertile habitat will encourage its vigorous growth. However, *P. chinense* grows in specific aquatic habitats, where oligotrophy and disturbance are combined, resulting in rather open vegetation with a low biomass. Also, judging by all plants with low fecundity of LL and all dead plants of ELL in light intensity treatment, *P. chinense* might not persist in such an environments with low percent PAR (field). Therefore, *P. chinense* should be a weak competitor restricted to peripheral habitats with reduced competition for space and light, similar to many other rare plant species. Ellenberg (1985) demonstrated that the relationship between a species'

indicator value for N of the habitat and its endangered status is the strongest among all of the examined indicator values among all Central European species. Lepš (2004) also noted that the most endangered species are those with the lowest N values of the habitat on average.

The capacity for tolerating both flooding and drought, and resilience after drawdowns is crucial for the successful establishment of riparian species in water-level-fluctuation zones (Silvertown et al. 2001; Luo et al. 2011). Locations where *P. chinense* are mostly distributed are sandy soils in waterside or shallow water environments in which flooding periodically occurs; sandy soils have a less moisture-retentive nature than clay and silt soils (Araya et al. 2011); the species is therefore forced to withstand both submerged and dry phases in this area. *P. chinense* were able to survive, grow, and reproduce under a wide range of hydrological circumstances, thus ensuring a persistence in the habitat. However, in water content treatment, total plant, rhizome, and seed dry mass had the highest value in HW. This indicates that environments in which the soil moisture content is not submerged in water and in which the distance from the water table is comparatively short might be favorite habitats for *P. chinense*. I observed in the following year that *P. chinense* submerged under 9 cm of water depth formed new shoots; on the other hand, the *P. chinense* completely submerged under 34 cm of water depth from July didn't elongate, make buds, or form any new shoot to rhizome. The findings of this observation shows that *P. chinense* could not be discovered in standing deep water, which is concurrent with the field survey, indicating the species could only inhabit environments where the water depth is limited to waterside or shallow water. Consequently, the realized width of niche for *P. chinense* is restricted by depth of water and attenuated light due to its competitors, so it could only have a narrow range of distribution. The elevational range on a water-level gradient inhabited by emergent macrophytes is usually determined by competitive interactions and the species' physiological response to flooding. Interspecific competition restricts the upper boundary, whereas flooding

tolerance determines a species' lower boundary, i.e. the maximum water depth at which a species can persist (Grace & Wetzel, 1981; Studer- Ehrensberger et al., 1993; Blom & Voeselek, 1996).

4.4 Synthesis regarding life historical strategies of P. chinense

P. chinense showed typical attributes of rare plants, which should be restricted to oligotrophic habitats with reduced competition for space and light and greater tolerance to nutrient deficits. Also, *P. chinense* could survive and reproduce under a wide range of hydrological environments from drought to waterlogged soils, and has a tolerance ability to drought, waterlogging, and submergence (15 days). This might have relevance to habitats where *P. chinense* mostly grows in sandy soils, in a waterside environment or in shallow water with periodic flooding.

N : P ratio of *P. chinense* (leaves : 6.66 ± 0.035 (n=3), stem : 3.14 ± 0.56 (n=6)) belongs to range of N limitation (N : P ratio < 14) (Koerselman and Meuleman 1996). Species with inherently low N : P ratios are predicted to dominate in N-limited vegetation, therefore, phosphorus fertilization should promote species with low N : P ratios (Güsewell, 2004). In addition, N : P ratio of *P. chinense* had low value just same as N:P ratio of ruderal species which has the lowest value among plant strategies. Also, ruderal species are often annual species or short-lived perennials with high reproductive allocation, leading to greater P requirements (Güsewell 2004). Reproductive allocation of *P. chinense* showed higher value (13.74 ± 0.34 g g⁻¹, n=6) than perennials mean (Reekie and Bazzaz 2011). In conclusion, *P. chinense* might have ruderal strategy. Grime's ruderal strategy is a general description of good colonists at a range of scales (Grime 1977). It characterizes plants associated with open, disturbed conditions and represents a heavy allocation to reproduction. Such species will perform well in bare areas where there is an abundance of microsites for establishment, but they will decline in the absence of disturbance (Pywell, Bullock et al. 2003). The distribution and life historical traits of *P. chinense* concur with ruderal strategy proposed Grime

(Yang and Kim 2015, unpublished manuscript). So, *P. chinense* might need flood in order to survive. Nutrient budgets and long-term management experiments have shown that the combination of haymaking and high N deposition increases net export of P from managed grasslands. Since this induces a shift from N limitation to P limitation in the long term (Güsewell, 2004), cutting competitor could well be negative to *P. chinense* with low N : P ratios. Floods allow for the maintenance of poorly competitive ruderal species like *P. chinense* (Bornette et al. 2001).

Sandy riparian rare plants that inhabit similar environments to that of *P. chinense* are expected to have analogous characteristics to *P. chinense*. So I hope our research is helpful to other studies for sandy riparian rare plants.

Identifying ecological traits of rare plant species different from those of common species has the potential to provide useful biological information for the management strategies aimed at the long-term conservation of rare plant species (Murray, Thrall et al. 2002). Murray, Thrall et al. (2002) suggested that the nature of relationships between rarity and ecological traits such as seed size, competitive ability, growth form, dispersal mode, and a suite of reproductive attributes are highly context-dependent. Thus autecological studies of rare plants continually need to advance. Although autecological studies are expensive and time-consuming, autecological studies revealed important aspects of the biology of particular rare plant species and such knowledge can be used effectively in management strategies for rare plant species. So the challenge for restoration and conservation ecology is to provide both contextual analyses that are relevant in particular situations and more general guidance that is broadly applicable—all of which assist in the endeavor of designing and implementing useful interventions and monitoring their effectiveness in the context of complex, rapidly changing environments (Hobbs and Cramer 2008).

4.5 The implication for the management of P. chinense

I suggest that *P. chinense* to be translocated to sandy soils that include

gravel in riparian areas where periodic floods occur (Fig. 5). All translocation approaches will rely on effective seed dispersal and natural regeneration to promote population growth and spread of rare plant (Jacobs, Dalgleish et al. 2013). So it is necessary to translocate *P. chinense* in riparian areas where periodic floods occur because it is a disturbance-dependent plant which re-establishes in a location where vegetation is removed due to flooding (Kimura et al. 2000); the realized niche width of *P. chinense* is also restricted to waterside or shallow water environments with periodic flooding. Such specific disturbance regimes can also increase richness of other weak competitive species (Zedler 2000). In addition, the reason I propose the translocation of *P. chinense* in sandy soils that include gravel is that this might be a more effective way to manage competitors. The characteristics of open habitats allow *P. chinense* to flourish because the species is a weak competitor. The results of an experiment in which *P. chinense* was transplanted to the waterside of a reservoir suggested that the removal of litter for germination and the removal of competitors in the growth stage are important for the perennial appearance of the species (Yonemura and Ihara 2008). This is because the seeds of *P. chinense* do not germinate in dark conditions such as when covered with leaves or soil (Yonemura 2000) and *P. chinense* is extirpated with increased competitors (Kang et al. 2003). Habitat specialists like *P. chinense* were indicated by high stress tolerance and were losing out more as time progressed in restored areas (Pywell, Bullock et al. 2003). Studies from Europe generally conclude that management is needed in order to prevent the extirpation of species characteristic of open wetlands (Scanga and Leopold 2012) and that post-planting management (e.g., fire, reduced competition) increases the probability of translocation success (Godefroid et al. 2011). However, while this type of artificial management method is a labor-intensive and costly process, translocating this species to sandy soils that include gravel could contribute to a reduction in the number of competitors, and require less labor and cost than artificial management. It is important to consider their relative costs and benefits because cost factors may render unrealistic or unachievable restoration

under current conditions (Hobbs and Cramer 2008).

Previous studies have shown that sandy soil containing a gravel concentration of greater than 10 percent by weight has a deleterious effect on root development and crop yields, seemingly due to the dilution of soil mass with the inclusion of gravel, resulting in low nutrient and water holding capacity (Babalola and Lal 1977). However, in gravelly soils, drought resistant crops are likely to perform better than drought sensitive crops (Grewal et al. 1984). Therefore, sandy soils that include gravel can be a relatively beneficial environment for *P. chinense* that is resistant to drought and nutrient deficit because this type of substrates inhibits the growth of competitive species. Also, gravel can mechanically impede the invasion of the roots and rhizomes of competitors because gravel produces symptoms typical of mechanical impedance (Babalola and Lal 1977). Moreover, during the times of flooding, gravels could help *P. chinense* to reduce the possibility of the uprooting by weighing down and to sustain longer. In both our work and in a previous study (Kang et al. 2003), it was observed that existing *P. chinense* communities with sediments were removed by flooding. In addition, sandy soils including gravel were found in Yongin, which is currently a *P. chinense* habitat. A number of *P. chinense* plants have been found in this area, indicating that during the life cycle of *P. chinense*, its seeds possibly germinate and the seedlings then grow and reproduce; the *P. chinense* population is able to become self-sustaining through the development of successive generations in this type of environment.

It is possible that sandy soils that contain gravel are suitable for riparian rare plant habitats. Wilsons Lake and Ellen-Wood Lake in the Tusket River system in Canada, Nova Scotia have sandy, gravel, and boulder shorelines characterized by remarkable species richness and the presence of many rare and endangered species (Wisheu and Keddy 1989). Selecting or creating infertile habitat recently began to grab attention from restoration science. Zedler (2000) suggested that at least one restoration site have insufficient nutrients like San Diego Bay (California, USA)

with coarse sandy soil which was leaky and supplied too little N to support tall plant because the diversity of restored wetland enhance species richness. And Pywell, Bullock et al. (2003) insisted that future work should focus on practical methods to increase the successful establishment of the poor performing but desirable species, and this might include addressing abiotic constraints, such as high residual soil fertility, by targeting sites for restoration with low fertility for a diverse species pool, a diversity of niches and enhancing opportunities of seedling recruitment (Pywell, Bullock et al. 2003). I hope that sandy soils with gravel which I proposed could be a good example for infertile site where rare plants could persist.

Ultimately, I proposed that further works are required to explore the ecological niche and tolerance to environmental conditions of rare plants that inhabit various environments and have different advantages. Furthermore, categorizing such ecological characteristics of rare plants based on habitat traits will be potentially of great benefit to practitioners and policy makers when they drew up and executed the plan to conserve and restore each rare plant. Because the rare plants of similar habitat are expected to have analogous ecological characteristics. Also, to categorize ecological characteristics of rare plants is expected to reduce the need for performing expensive and time-consuming studies for every rare plant species. I believe that my research could be a good starting point for study of the translocation of rare plants to suitable sites.

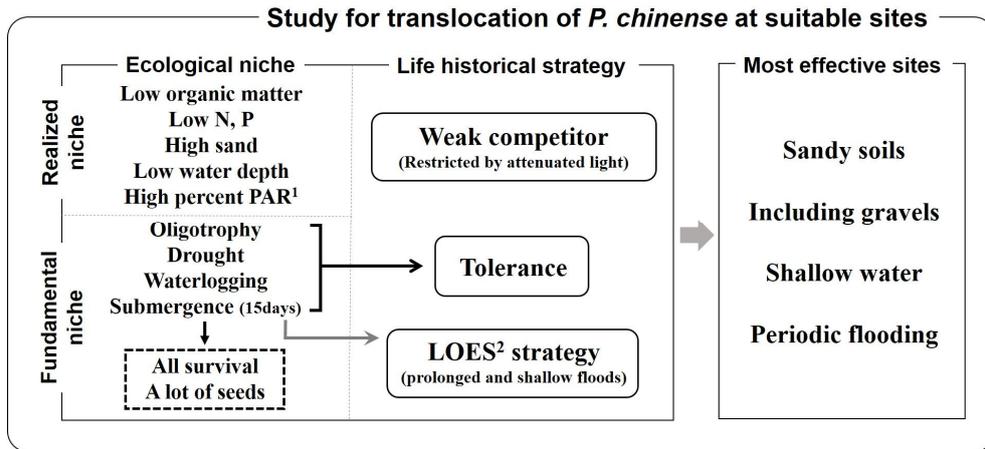


Fig. 6 Schematic diagram representing the ecological niche, tolerance to soil nutrient deficit, drought, waterlogging, and submergence of 15 days and most effective sites for the translocation of *P. chinense*.

¹Percent PAR: Photosynthetically active radiation of respective quadrats / photosynthetically active radiation of full light at the open air surrounding.

²LOES: Low Oxygen Escape Syndrome.

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국문초록

새로운 환경에 옮겨 심기는 희귀 식물 종의 보존을 위한 필수적인 방법이다. 이런 노력의 일반적인 실패 원인은 주로 적합하지 않은 새로운 장소에 옮겨 심었기 때문이다. 본 연구에서는 주로 모래 땅 수변에 서식하는 희귀 식물인 낙지다리(*Penthorum chinense*)의 성공적인 옮겨 심기를 위해서 낙지다리의 실현지위, 기본지위, 환경 조건들에 대한 내성을 이해하고자 야외조사와 메조코즘 실험을 실시하였다. 낙지다리 분포의 환경 범위는 상대적으로 낮은 천이도 (9.02~1031), 높은 광합성 활성 빛 세기의 상대적인 비율 (11.94~100 %), 낮은 토양 유기물 양 (0.89~4.38 %), 낮은 $\text{NO}_3\text{-N}$ ($0.04\sim 12.61 \text{ mg kg}^{-1}$), 낮은 $\text{PO}_4\text{-P}$ ($0.75\sim 28.42 \text{ mg kg}^{-1}$), 많은 모래 비율 (13.85~94.98 %)을 가지며 낮은 수심이나 물가에서 서식하고 (-9~7 cm), 포화된 땅에서 건조한 땅까지 넓은 범위의 토양 수분함량의 땅에서 발견되며 주기적으로 범람이 일어나는 지역에서 산다. 메조코즘 실험에서 극도로 낮은 빛 환경 ELL)을 제외하고 모든 식물이 생존했고 자랐고 종자와 지하경을 통해 번식하였다. 게다가 낮은 빛 환경 (LL)을 제외하고 심한 스트레스 환경에서도 종자 수와 발아율이 심하게 감소하지는 않았다. 실험 결과는 낙지다리가 양분이 적고 교란이 있는 좁은 실현지위를 가지며, 토양 양분과 토양 수분 양에 대해서는 기본지위가 넓은 것을 보여주었다. 또한 낙지다리는 양분 부족, 건조, 토양의 수분 포화, 15일 간의 침수 조건에서 내성이 있음을 나타내는 다양한 특징을 보였다. 따라서 낙지다리가 식물 생산성이 낮은 주변 지역으로의 제한적인 분포를 보이는 것은 다른 희귀 식물 종에서 주로 나타나는 현상과 마찬가지로 빛에 대한 경쟁을 감소시키려는 전략일 것이다. 그리고 낙지다리는 범람과 건조가 번갈아 일어나는 수변 지역에서의 생존을 증가시키는 전략을 가지고 있는 것으로 여겨진다. 이와 같은 낙지다리의 생태적 특징을 바탕으로 낙지다리는 물가나 얕은 물의 주기적인 범람이

일어나는 지역의 자갈이 포함된 모래 땅에 옮겨 심는 것을 제안한다. 이러한 환경은 토양 양분과 수분 수용량이 낮아서 다른 경쟁식물들의 생육을 심하게 저해하는 반면 낙지다리는 이러한 환경 조건에 대해 내성이 있으므로 경쟁에서 우위를 차지할 수 있을 것으로 여겨진다. 본 연구는 희귀 식물을 적합한 장소에 옮겨 심기 전에 수행해야 할 그 식물의 생태적 특징을 이해하기 위한 연구로서 좋은 출발점이 되리라 믿는다.

주요어 : 기본지위, 낙지다리, 내성, 실현지위, 옮겨 심기, 자갈, 재도입

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