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Original Research

The life history strategy of *Penthorum chinense*: Implication for the restoration of early successional species

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ABSTRACT

The ecological importance of early successional ecosystems has received little attention. Especially, few studies have reported the life history traits and management of early successional herbaceous plant species in riparian zones. Our study was designed to determine whether: (1) the riparian pioneer herbaceous plant *Penthorum chinense* has tolerance to droughts and floods as pioneer tree species and (2) *P. chinense* is highly capable to resist infertile soil to avoid low light conditions due to weaker competitive ability than pioneer tree species. We performed mesocosm experiments and field surveys to understand the tolerance to stressful environments and the ecological niche of *P. chinense*. The following parameters showed the plant's stress tolerance: (i) Root mass fraction and N concentration of stem to nutrient deficit. (ii) Root mass fraction, chlorophyll amount, and N concentration of stem to drought. (iii) Root dry mass and N concentration of stem to waterlogging. (iv) Height per total plant mass, specific leaf area, time to flowering, seed mass fraction, rhizome mass fraction, and chlorophyll amount to submergence of 15 days. The results indicate that *P. chinense* shows tolerance to nutrient deficit, drought, waterlogging and submergence of 15 days. Also, *P. chinense* has a narrow realized niche that requires oligotrophy and disturbance. The restricted distribution of *P. chinense* to low-productive infertile soils might be a strategy to reduce competition for light. Moreover, *P. chinense* has the strategy to increase survival in habitats that have alternate occurrences of flooding and drought. Herein, we suggest translocation of *P. chinense*, assessed as a least concerned species in Korea and a vulnerable species in Japan, to sandy soils that include gravel in waterside environments or shallow waters with periodic flooding for restoration.

1. Introduction

Early successional ecosystems show great diversity in the abundance of plant and animal species (Fontaine et al., 2009). In many ecosystems subject to disturbances, early succession is the only period when tree canopies do not dominate, and so this stage can be characterized by high productivity of plant species, complex food webs, large nutrient fluxes, and high structural and spatial complexity at small scales (Swanson et al., 2011). Early successional plant communities enhance nesting and protective brooding cover and produce a quality food source for many wildlife species (Nam et al., 2008). However, early successional species are endangered not only because of the intensification of farming and declining numbers of pastures, hay meadows and abandoned fields, but also because of the suppression of natural disturbances such as fires, beaver activity, wind storms and floods. Moreover, there is little knowledge on the autecology of pioneer species despite the importance of early successional ecosystems for biodiversity (Goodale et al., 2012). Early successional ecosystems could be appropriately considered by resource managers and scientists, and included within management/research programs dedicated to maintaining the functions of early successional ecosystems, e.g. making environmental conditions more favourable for plant and animal species of next seral stages, and providing habitats for endangered species (Swanson et al., 2011; Jeong and Kim, 2017).

Some of the differences between early and late successional species in agricultural fields, prairie, forests, and dunes have been well documented (Byun et al., 2008). Net primary production and net photosynthetic rates decrease as succession proceeds (Bazzaz, 1979). Early successional species have greater performance in resource-rich portions of gradients, namely high light, high nutrients and moderate to high moisture, than late successional species (Zangerl and Bazzaz, 1983). In addition, early successional plants have broader responses and higher similarity in niche axes of

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underground space, soil moisture, and soil nutrient concentration than late successional plants (Parrish and Bazzaz, 1982). The physiological and morphological plasticity in response to a varying environment are important adaptive characteristics of early successional species and are consistent with the varying environment found in early successional habitats (Bazzaz and Carlson, 1982). Moreover, early successional species reportedly devote more resources to reproduction and less to below-ground biomass relative to later successional species (Zangerl and Bazzaz, 1983; Yang and Kim, 2016).

Wetlands are a major type of ecosystems affected by humans, and are currently in the process of being restored; moreover, the monetary value of wetland functions is particularly high (Zedler, 2000). Especially, the riparian zones are a key factor in the biodiversity of wetlands (Zweig and Kitchens, 2009), because typical wetland succession is initiated by a partial or total disturbance in riparian zones (Platt and Connell, 2003). Therefore, research on early successional plant species in riparian zones is crucial for the maintenance of biodiversity and wetland functions in riparian zones.

A few studies have focused on the life history traits of pioneer tree species in riparian zones. Willow (*Salix humboldtiana* Willd.) and South American alder (*Tessaria integrifolia* Ruiz et Pav.) have high ability to resist droughts and floods, even in extreme hydrological conditions, due to structures and processes that allow them to persist in this landscape (Neiff, 2005; Casco et al., 2010). The European black poplar (*Populus nigra* L.) is strictly heliophilous, and forms metapopulations by colonizing open areas (Zsuffa, 1974; Herpka, 1986; Lefèvre et al., 1998). Similarly, two species of evergreen pioneer trees, *Senna reticulata* and *Cecropia latiloba*, colonize open areas very successfully in floodplains due to their flood tolerance, although they colonize different inundation gradients in the floodplains (Parolin, 1999). Moreover, waterlogged trees and seedlings of *Senna reticulata* are characterized by extremely high photosynthetic assimilation and growth. In waterlogged seedlings in a flooding experiment, *Senna reticulata* produced adventitious roots and lenticels indicative of very efficient and well-adapted inhabitation of floodplains. In addition, *Senna reticulata* is most competitive on sunny, open spaces with high nutrient content (Parolin, 2001).

However, few studies have reported the life history traits of early successional herbaceous plant species in riparian zones (Hong et al., 2012; Kim et al., 2012; Shin et al., 2015). Herein, we selected *Penthorum chinense* Pursh, a pioneer herbaceous plant species that inhabits mainly riparian zones. The study was designed to determine whether: (1) the pioneer herbaceous plant has similar tolerance to droughts and floods as pioneer tree species and (2) the pioneer herbaceous plant is highly capable to resist infertile soil to avoid low light conditions due to weaker competitive ability than pioneer tree species. We accordingly conducted laboratory experiments of soil nutrient content, soil water content, submergence and post-submergence and investigated the environmental range for the distribution of *P. chinense* in the field to figure out the life history strategy of *P. chinense* with respect to mass allocation, flowering time and growth rate as dependent on nutrient supply, drought, waterlogging, and submergence. Based on the study results, we propose the most suitable measures for restoration of *P. chinense*.

2. Material and methods

2.1. Study species

Penthorum chinense is a pseudo-annual plant frequently distributed in riparian flood plains, marshes, wetlands around paddy fields, and abandoned paddy fields in eastern Asia, which reproduces sexually by seeds and vegetatively by rhizomes (Yonemura, 2000; Ikeda and Itoh, 2001). Currently, *P. chinense* populations have been decreasing due to habitat destruction caused by river trimming, 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, 2016) and as a vulnerable species in Japan (Japanese Ministry of the Environment, 2016).

2.2. Sampling and cultivation of plants

Rhizomes of *P. chinense* were collected from a natural population at a waterside site in Hongsung, Chungcheong-Nam do, Korea. Since the collection was inadequate due to the rarity of *P. chinense*, we purchased rhizomes of *P. chinense* that were cultivated adjacent to a paddy field in Gangneung, Gangwon do, Korea. These 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), excepting the nutrient reduction treatment samples, which were transplanted to containers (3.5 cm wide, 5.5 cm long, and 10 cm deep) for hydroponics. Collected rhizomes were used for nutrient reduction treatment and submergence and post-submergence treatment, whereas purchased rhizomes were used for soil water content treatment. One plant was transplanted to each pot or container. Each group had six replicates. Fresh weight and shoot length of each plant obtained prior to transplantation was considered in the setup of the experiment.

2.3. Mesocosm experiment

Treatments were initiated at one week after transplanting to allow for acclimatization. Position of the pots were completely randomized and rotated at least monthly so that all plants experienced the same environmental conditions within each treatment. Individual treatments were performed for different lengths of time as follows: Nutrient reduction treatment from July to October, soil water content treatment from June to October, submergence treatment for 15 days in July and post-submergence treatment from July to October 2012. Plants were harvested in October, when all plants had completed fruit production. The air temperature and relative humidity in the greenhouse were maintained between 1.0 and 37.2 °C and 21.6 and 100.0%, respectively (Suppl. Fig. A.1, 2), and measured hourly by Hobo data logger (Part U23-001, Onset Corp., Pocasset, MA) during the period of June to October 2012. The photosynthetic photon flux density (PPFD, 204–1488 $\mu mol\ m^{-2}\ s^{-1}$) was recorded between 12:00 and 13:00 Korean standard time (KST), during the same period of June to October 2012 (Suppl. Fig. A.3).

2.3.1. Nutrient reduction treatment

Initially, nitrogen concentrations alone were adjusted with full strength modified Hoagland's solution (Shipley and Keddy, 1988) up to 0.9 mM (N10 group); subsequently, solution of the N10 group was diluted with deionized water to obtain three nitrogen concentrations, viz. 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. A cover was placed over each container to minimize evaporation and reduce algal growth in the nutrient solution. The concentrations of NO_3-N and PO_4-P (mM) in the solutions for hydroponics were selected from the concentrations of extractable NO_3-N and PO_4-P ($mg\ kg^{-1}$) in soil at the habitat. NO_3-N and PO_4-P concentrations for the N10 group, 1/3 group, and 1/100 group in hydroponics were similar to the maximum values, mean value, and minimal vales of extractable