Flora 206 (2011) 935–942

Contents lists available at ScienceDirect

Flora

journal homepage: www.elsevier.de/flora

Seed vigor and plant competitiveness resulting from seeds of *Eupatorium adenophorum* in a persistent soil seed bank

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ARTICLE INFO

Article history:
Received 17 January 2011
Accepted 8 April 2011

Keywords:
Competitive ability
Eupatorium adenophorum
Germination
Persistent soil seed banks

ABSTRACT

Seeds in a persistent soil seed bank (PSSB) provide an effective way to maintain plant population and community stability. Seeds that persist in soil incur physiological costs of maintaining viability and vigor, thus, the growth capability of resulting plants may be reduced. However, a lot of functional roles of the PSSB have been deduced from seed germination capability, and little consideration has been given to interspecific and intraspecific competitive ability of the resulting plants. *Eupatorium adenophorum* was used as the study species to compare germination of different artificially aged PSSB seeds and competition at different densities between resulting plants of aged and freshly produced seeds. Seed burial caused decreases in survival rates but not germination speed. During the 175-day growth period, the individual biomass, average height, basal stem diameter and leaf number of plants from aged PSSB seeds were little lower than that of plants germinated from freshly produced seeds. However, the differences were not significant at any densities. Thus, (1) although seeds stored in soil exhibited a very high death rate, they maintained a high vigor for germination, and (2) resulting plants from PSSB seeds exhibited good competiveness to plants from new seeds of the same population. The results further confirm the significance of PSSB in maintaining stability of plant populations and communities.

Introduction

The soil seed bank is a reserve of mature viable seeds located on the soil surface or buried in soil, duff or litter (Roberts, 1981). When a seed arrives at the soil surface, it may germinate immediately or persist in the soil for a short or long period. With respect to the different lengths of time seeds remain viable and ungerminated in the soil, soil seed banks have been classified as (1) transient soil seed banks (TSSB), when seeds persist in the soil for ≤1 year or ≤1 germination season; and (2) persistent soil seed banks (PSSB), when they persist in the soil for at least 1 year or until the second germination season (Thompson and Grime, 1979; Walck et al., 2005). The ability of seeds to persistence in a soil seed bank has been used as an important functional trait to classify regeneration strategies (Grime and Hillier, 2000).

The PSSB is an important viable evolutionary strategy and a life history countermeasure to variable environment conditions. Baskin and Baskin (1998) reported that there are more than 1300 species from 160 families that can form PSSB. Seeds in the PSSB retain vigor in soil for years or decades, depending on their dormancy or quiescence state (Murdoch and Ellis, 2000). Why should seeds persist in the soil? Bet-hedging strategy has been a popular hypothesis that has been used to explain persistence of PSSB seeds for many years. Thus, it is a mechanism by which plants, especially annuals can reduce risk of extinction through germination when reproduction fails in a risky environment (Baskin and Baskin, 1998; Philippi, 1993; Thompson, 2000; Venable and Brown, 1988). Some studies also suggest that the PSSB can help maintain population stability and conserve genetic diversity (Baskin and Baskin, 1998; Mandák and Plačková, 2009). In addition, the PSSB could be most advantageous in communities of annual plants occupying habitats that experience frequent catastrophic events (Fenner and Thompson, 2005). In such cases some invasive species or farm weeds can extend their invasion time and range by increasing the density of propagules (Shen et al., 2006).

However, the significance of these functions of the PSSB is based on the assumption that PSSB seeds still have enough vigor to maintain competitiveness of the resulting plant, both at the interspecific and the intraspecific level. Survival and growth with weak competitive ability would reduce the chances for reproductive success and maintenance of genetic diversity, thus reducing the ecological significance of the PSSB. In fact, seeds that persist in soil will incur material and physiological costs to the challenge of death. The time required for germination and emergence of plants from

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doi:10.1016/j.flora.2011.07.002

aged seeds stored under room conditions was greater than that of fresh seeds in agricultural species (Wang and Zhao, 1990; Xu, 2006). Relative to seeds stored under room conditions, those stored in the soil may face more threat to death and need to incur more physiological costs (Kivilaan and Bandurski, 1981; Telewski and Zeevaart, 2002). Under natural conditions, the resulting PSSB plants will be confronted with intense competition from their siblings produced from differently aged seed cohorts or from plants of other species. Thus a decline of seed vigor could result in delayed germination, retarding seedling establishment while the probability of site preemption by other plants is increasing with time. This could result in reduced growth of PSSB plants, leading to smaller adult size and reduced reproductive output (Rees, 1994; Roach and Wulff, 1987).

In 1879 Beal, at Michigan Agricult. College, initiated as the first scientist a burial study to determine seed longevity in the soil under natural conditions (Kivilaan and Bandurski, 1981; Telewski and Zeevaart, 2002). Following Beal, a lot of burial experiments were extended to other species to test seed persistence (e.g., Hill and Van der Kloet, 2005; Holmes and Newton, 2004; Kalisz, 1991; Schwienbacher et al., 2010). These studies mainly focused on seed viability, and only a few of them considered reproduction of resulting plants (Telewski and Zeevaart, 2002). However, none of them paid attention to the competitive ability of the resulting PSSB plants.

We hypothesized that aging would cause a decrease in survival rate and that plants from PSSB seeds would be less competitive than those from fresh seeds of the same population. To test this, seeds of an invasive species were aged in the soil for 1–4 years. Germination was tested every year and competition between plants resulting from 3-year-old PSSB seeds and plants from freshly produced seeds was tested at different densities to examine whether there was any delay in germination of a seed cohort and whether the competitive ability of resulting PSSB plants was reduced. To our knowledge, this work is the first direct test of competitive ability of resulting plants of PSSB seeds.

Materials and methods

Study species

Eupatorium adenophorum Spreng. is a multi-stemmed erect perennial herb of the family Asteraceae (Baruah et al., 1994) that was introduced from its native range of occurrence in Mexico to Europe, Australia and Asia as an ornamental species. Now, it is widely distributed in over 30 countries and regions (Qiang, 1998). In Asia, the species spread from Burma into Yunnan province of China in the 1940s. Since then, it has proliferated extensively and has became a serious aggressive weed in southwest China, having a grave impact on the ecology, environment, economic development and human health of the people in Yunnan, Guizhou, Guangxi and Sichuan provinces (Sun et al., 2006; Vitousek, 1990). Seeds of *E. adenophorum* mature in April in southern China, and it is one of the plant species found in China that forms a PSSB (Shen et al., 2006). Thus we selected it as our study species to investigate the effect of seed aging under natural conditions on germination and competitive ability of resulting PSSB plants.

Seed collection and burial

A vigorously growing and productive *E. adenophorum* population at Xishan Park in Kunming city, Yunnan (24°58′39″N, 102°36′33″E) with ca. 200 individuals was selected as the source of mother plants. Ripe seeds were collected from this site in April 2003. After collection, 100 air-dry seeds were enclosed in nylon mesh bags (0.2 mm) and buried in soil group by group to create an artificial persistent soil seed bank (PSSB) at an open site at Kunming Section of the Xishuangbanna Tropical Botanical Garden (XTBG Kunming), ca. 10 km from the seed collection site and at the same altitude. Every group included three burial depths (0, 5 and 10 cm), and 15 replications were used per depth. For comparison, we also stored some seeds under dry condition in the laboratory of XTBG Kunming to create aged seeds as a check (CK) when PSSB seeds were prepared. Seeds were collected again in 2009 for competition test.

Mean annual precipitation in Kunming (at 1891 m a.s.l.) is 1035 mm, 88% of which falls between May and October. Mean annual temperature is 14.5 °C, mean maximum temperature 19.7 °C (July) and mean minimum temperature 7.5 °C (January).

Germination test

A subsample of freshly sampled ("new"), CK, and aged PSSB seeds, the latter buried for 1, 2, 3 and 4 years, were used to determine survival rate. Each test contained 5 replicates of 100 seeds per buried depth. After 10 min sterilization in 1% NaClO solution followed by three rinsings with distilled water, seeds were transferred into Petri dishes filled with 1% agar (10 g/l) and placed in a growth cabinet providing 12-h light with 8000 lx illuminance at 25 °C and 12-h darkness at 15 °C. Germination (radicle emergence) was recorded every day for 3 weeks.

Competition between plants resulting from germination of 3-year-old PSSB seeds and fresh seeds, respectively

Competition studies were conducted in the 2009 growing season in an unheated greenhouse at XTBG Kunming. Laterite soil from the seed collection area was mixed with humus (2:1, v/v) and then sterilized for 8 h at 105 °C in an oven. This soil contained 4 mg/kg available nitrogen, 3 mg/kg available phosphorus, 200 mg/kg available potassium and 93 g/kg organic matter. Soil pH was 6.8. Plastic pots 15 cm (diameter) × 15 cm (depth) were filled with 1600 g weighted sterilized soil, to approximately 2 cm below the top of the pot.

There were six treatments in this experiment, including two controls and four competition densities. Each treatment was replicated 15 times, for a total of 90 pots. In June 2009, fresh seeds and seeds buried in 2006 (3 years old) were sterilized in 1% NaClO solution for 10 min, washed three times with distilled water and then transferred into Petri dishes for germination. For controls, in a reciprocal way one seedling resulting from 3-year PSSB seeds or from new seeds was planted in the center of the pot. A grid orientation design was adopted to control four densities of the other plants in a pot: the center of the soil surface of each pot was taken as a basic point, and then the soil surface (144 cm^2) was gridded by using different sizes of iron mesh, yielding different grid sizes and tiers in the pot. In each pot, a 3-year PSSB seedling (hereafter PSSB plants) was planted at the central point, and four seedlings that germinated from new seeds were placed at the first tier of the grid as observation plants (hereafter observation plants) for different densities (Fig. 1). In treatment of 0.1, 0.17, 0.6 and 2.17 plants/cm^2, the four observation plants were planted diagonally. Other plants used for the four densities were germinated directly in the pots simultaneously as PSSB seedlings and observation seedlings from seeds that were placed following the grid ("sown plants"). To assure establishment of these plants, three seeds were sown into each grid position and then randomly thinned to a single plant after emergence.

The resulting PSSB plants and the observation plants that died after transplanting were replaced with individuals of comparable size during the first 2 weeks. Pots were placed randomly in the greenhouse, and their positions were shifted every 2 weeks