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ISSN 0367-2530
Flora · 206(2011)11
pp. 921–996

Volume 206 · 2011 **11**

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

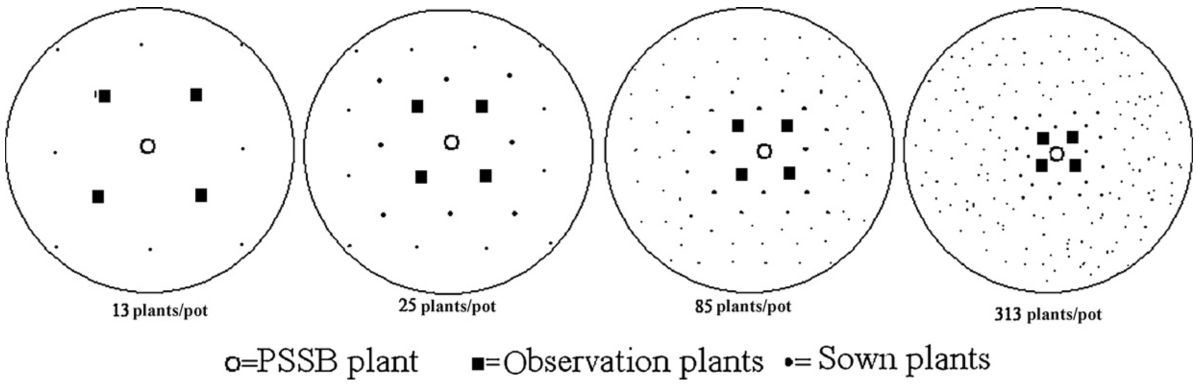

Fig. 1. Diagrams showing the arrangement between plants resulting from 3-year PSSB seeds and from fresh seeds (Observation plants and Sown plants) for different density treatments.

to reduce micro-environmental effects. Soil was watered to field capacity each day.

Biomass was measured at 30-day intervals from 17 June 2009 (32 days after germination) to 30 October 2009. At each harvest, three pots of each density were randomly sampled. The resulting PSSB plants and observation plants were marked and separated from other plants by washing with water, and then they were dried separately at 80 °C for 24 h and weighed. There were a total of five harvests. Height, basal stem diameter and number of leaves of resulting 3-year PSSB plants and observation plants germinated from new seeds were measured at 15-day intervals for all of the remains after harvest.

Data analysis

The following indices were used to evaluate survival and germination of seeds.

(1) Survival rate (SR) = $\sum G/N \times 100$, where G is the number of seeds germinated and N is the number of seeds tested;
(2) Days to first germination (DFG);
(3) Time of maximum germination (TMG); and
(4) Mean time to germinate (MTG) = $\sum(Gi \times Di)/\sum Gi$, where Gi is the number of seeds germinated at i days (Di).

Repeated measures ANOVA with burial depth as fixed treatment factor and time as the repeated measures factor was applied to test the significance ($p < 0.05$) of difference of mean survival rate (SR) of different burial depth and time. Further comparison of SR differences between different depth at the same burial time, between different time at the same depth were performed by Student–Newman–Keuls (S–N–K, $p < 0.05$) test. Values of mean biomass, genet height, basal stem diameter or number of leaves of plants of PSSB 3-year seeds and of new seeds of the same pot at each measurement time were paired and then a paired samples t-test was applied to check the significance of differences after splitting data by density. All analyses were performed with SPSS 13.0, and figures were produced with SigmaPlot 10.0.

Results

Germination

The survival rates (SR) of PSSB seeds of *Eupatorium adenophorum* were significantly different among different burial time and among different burial depth (Repeated measures ANOVA, $p < 0.05$). The SR at depths of 0 cm, 5 cm and 10 cm decreased significantly

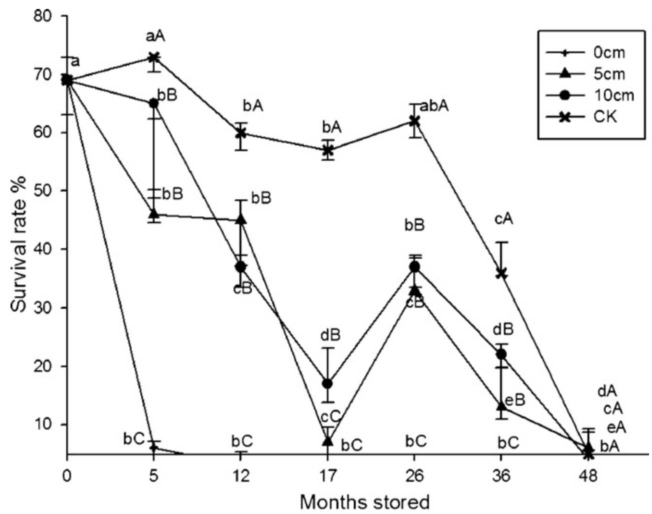

Fig. 2. Survival rate of *E. adenophorum* seeds after different times of soil burial and room temperature storage (CK), respectively (%, mean ± SE). Values with different lowercase letters within the same line and values with different uppercase letters among different burial depth differ significantly (one-way ANOVA, $p < 0.05$).

as the burial time increased, and these percentages were significantly smaller than that of CK (Fig. 2). SR at 0 cm depth was lower than SR at depths of 5 and 10 cm. However, the difference between SR at 5 cm and 10 cm was significant only at 17 months. Ninety percent of seeds buried 5 months at 0 cm depth were dead. Forty percent of seeds were viable at depths of 5 cm and 10 cm after 2 years, and 20% of seeds still could germinate after 3 years (Fig. 2). Up to the fourth year, survival rates at 5 and 10 cm decreased to less than 10%. Survival rate of seeds stored dry in laboratory did not differ significantly from that of the original percentage after 26 months (ca. 2 years). However, SR decreased to 40% after 3 years storage, and 90% of the seeds had lost viability at year 4 (Fig. 2).

Seeds stored dry in laboratory for 5 months exhibited a delay in germination. Their time for maximum germination and mean time to germinate was delayed one day compared with seeds buried in soil (Table 1). After storage for 3 years in laboratory, the still viable seeds in laboratory germinated 6 days after planting, time for maximum germination was reached at days 13–14 and mean time to germinate was >12 days. In soil aged seeds (PSSB seeds) germinated 3 days after planting, and neither time for maximum germination nor mean time to germinate changed with burial time (Table 1).

Table 1
Days to first germination (DFG), time of maximum germination (TMG) and mean time to germinate (MTG) of *Eupatorium adenophorum* seeds (days) buried at different depths in soil and stored in laboratory (CK).

	Depth (cm)	Time after burial (months)						
		0	5	12	17	26	36	48
DFG	0	3	3	4	–	–	–	–
	5	3	3	3	3	3	3	3
	10	3	3	3	3	3	3	3
	CK	3	3	3	3	6	7	7
TMG	0	3–4	3–4	3–4	–	–	–	–
	5	3–4	3–4	3–4	3–4	3–4	3–4	3–4
	10	3–4	3–4	3–4	3–4	3–4	3–4	3–4
	CK	3–4	4–5	4–5	6–7	9–10	13–14	15–16
MTG	0	5.24	8.06	6.98	–	–	–	–
	5	5.24	4.50	4.52	6.50	4.72	5.05	4.12
	10	5.24	3.97	4.26	4.54	4.24	4.43	4.36
	CK	5.24	6.66	5.57	9.77	11.15	12.86	18.32

Competition

Total dry biomass of *E. adenophorum* per pot increased with increase in time after planting (Fig. 3). At early growth stage, this total biomass was affected by density. However, after 117 days, biomass per pot did not differ significantly among densities of 13, 25, 85 and 313 plants per pot (Fig. 3). Biomass of individual plants resulting from 3-year-old PSSB and plants resulting from new seeds varied significantly among different densities over the growth period ($p < 0.01$, two-way ANOVA), and this variation increased with increase in growth time. At early stage, average difference in biomass among different densities was not great. However, with increase in time after planting, this difference increased. Although the biomass of individuals of plants resulting from new seeds was higher than that of plants resulting from 3-year-old PSSB under intense competition (Fig. 4), these differences were seldom significant (t-test, $p > 0.05$) at the same sampling time.

Mean height of *E. adenophorum* genets both resulting from PSSB seeds and from new seeds increased with increase in time after planting (Fig. 5), but it decreased with increase in density at any sampling time ($p < 0.01$, two-way ANOVA). The differences among different densities increased with increase in time after planting. In most circumstances and across all densities, especially at the higher densities (85 plants/pot and 313 plants/pot, Fig. 5) the mean height of individuals of plants resulting from new seeds was a little higher than that of plants resulting from 3-year-old PSSB. However, these differences were seldom significant at the same sampling time (t-test, $p > 0.05$).

Mean basal stem diameter and number of leaves of plants resulting from 3-year-old PSSB seeds and from new seeds, respectively, had the same pattern of seasonal change as height of these plants. Both parameters were significantly affected by density ($p < 0.01$, two-way ANOVA). The differences among different densities increased with progress in time after planting. Mean basal stem diameter and number of leaves per plant decreased significantly with increase in density. The basal stem diameter and number of leaves from plants resulting from 3-year-old PSSB were smaller than those of plants resulting from new seeds under most circumstances and across all densities (Figs. 6 and 7). However, these differences were seldom significant at the same sampling times (t-test, $p > 0.05$).

Discussion

A burial experiment is the most effective way to document seed longevity of PSSB. Beals' burial experiment indicated that seeds of *Verbascum blattaria* continued to exhibit high viability (50%) after 120-year (Kivilaan and Bandurski, 1981; Telewski and Zeevaart, 2002). *Eupatorium adenophorum* seeds can survive for only one germination season (ca. 5 months from maturation) on the soil surface, but they can survive for 4 years at 5 and 10 cm soil depths and under dry storage condition in laboratory. Thus, seeds of this species have a longevity of ca. 4 years in the soil. The high reduction in survival rate during the storage period indicates the high risk of death during this timespan. A similar tendency for reduction of survival rate was also observed by Holmes and Newton (2004) for different seed types after burial for 3 years.

A distinct difference both in survival rate and germination speed was found in this study between seeds buried in the soil and seeds stored under dry condition in the laboratory. The survival rate of buried seeds was lower than that of seeds in dry storage. However, the days to first germination, the time when maximum germination occurs, and the mean time to germinate increased with increase of storage time in seeds stored dry. These indices did not change with increase in burial time for PSSB seeds (Table 1). The differences between seeds in dry and in soil storage may result from the different temperature and moisture conditions under the two storage treatments. Harrington (1972) suggested that a 1% reduction in seed moisture content, or a 5 °C reduction in temperature during storage can doubles the length of life of seeds in dry storage. Seeds buried in soil (high moisture and high temperature in germination

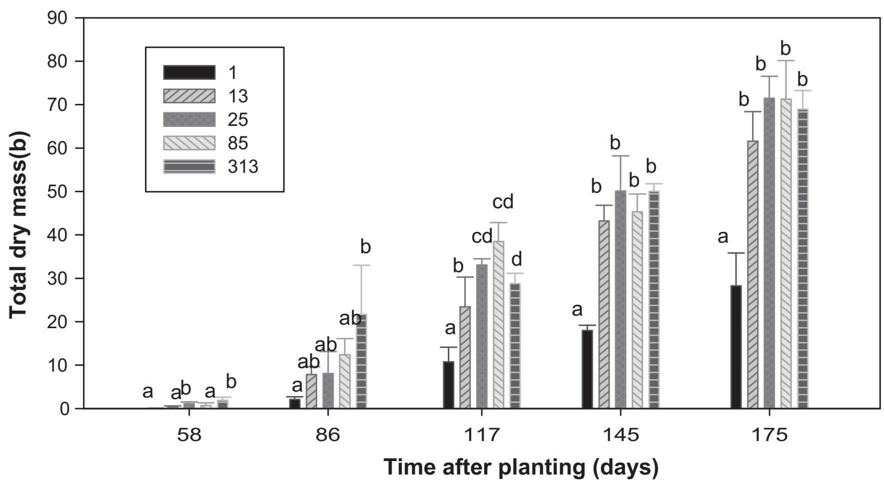

Fig. 3. The total biomass yield (g dry mass) of *E. adenophorum* (all plants in a pot) at different densities (plants/pot; insert) during the whole growing season. Values with different lowercase letters within the same time period differ significantly (one-way ANOVA, $p < 0.05$).

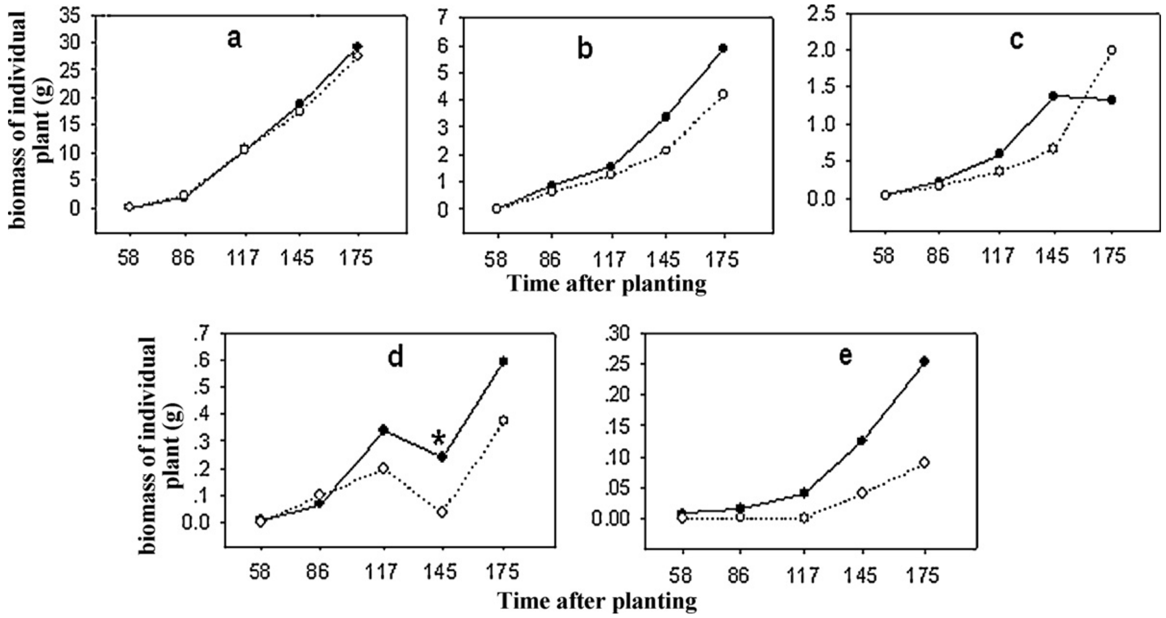

Fig. 4. Biomass at end of the growing season of individual plants resulting from 3-year-old PSSB (○) and freshly produced seeds (●), respectively, developed at different densities (a: 1 plant/pot; b: 13 plants/pot; c: 25 plants/pot; d: 85 plants/pot; e: 313 plants/pot). *Biomass at the same sampling time significantly different (*t*-test, $p < 0.05$).

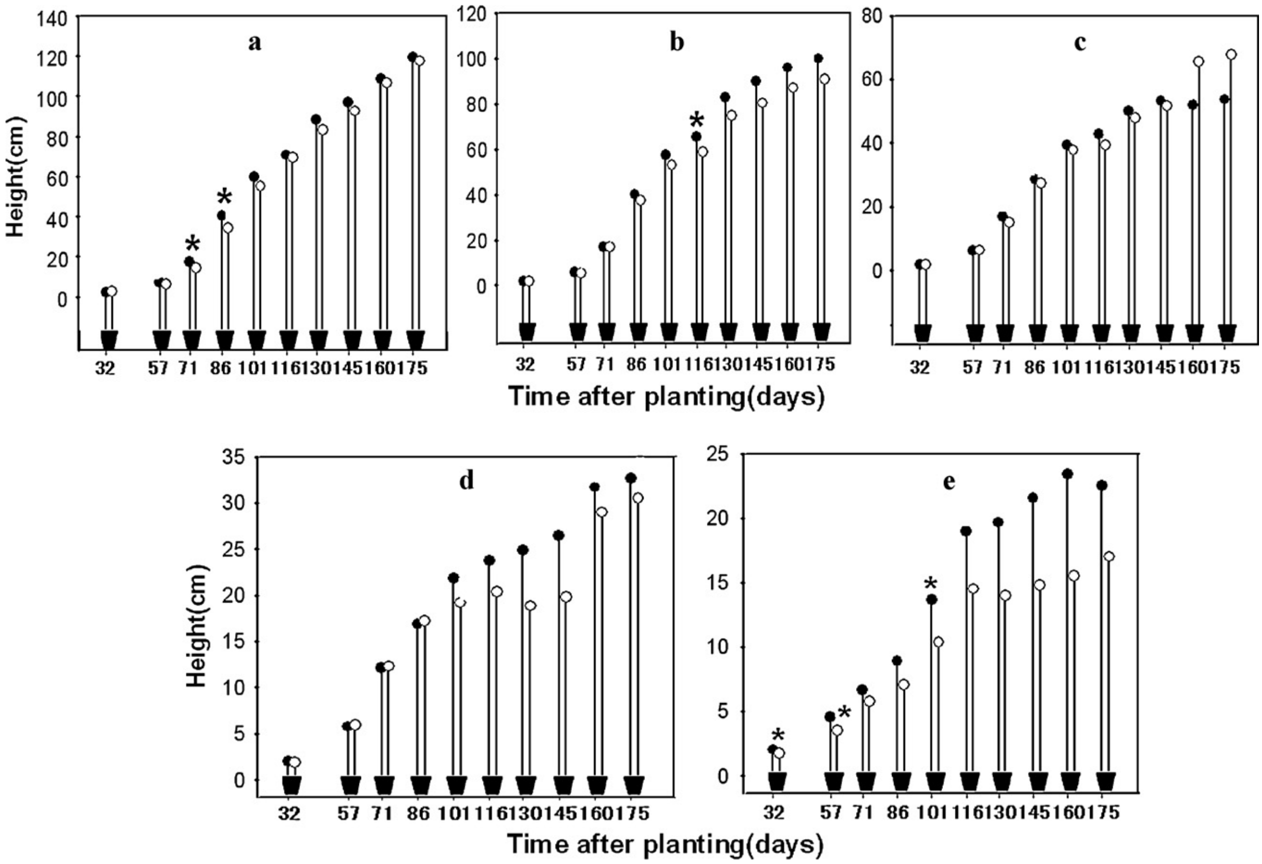

Fig. 5. Mean height of plants resulting from 3-year-old PSSB (○) and from freshly produced seeds (●) at different densities (a: 1 plant/pot; b: 13 plants/pot; c: 25 plants/pot; d: 85 plants/pot; e: 313 plants/pot) during the whole growing season. *Plant height between plants resulting from of 3-year aged PSSB seeds and those from new seeds significantly different at the same sampling time (*t*-test, $p < 0.05$).

season) face high damage and high probability of death, but those that survive have a better germination behavior. In other words, there may be a threshold for seed vigor in relation to the resources and physiological costs in seeds. Once the resource investment and the physiological costs exceed the threshold, seeds would die whether stored in soil or under dry conditions.

Eupatorium adenophorum plants competed with each other at sowing densities of 13, 25, 85 and 313 individuals per pot.

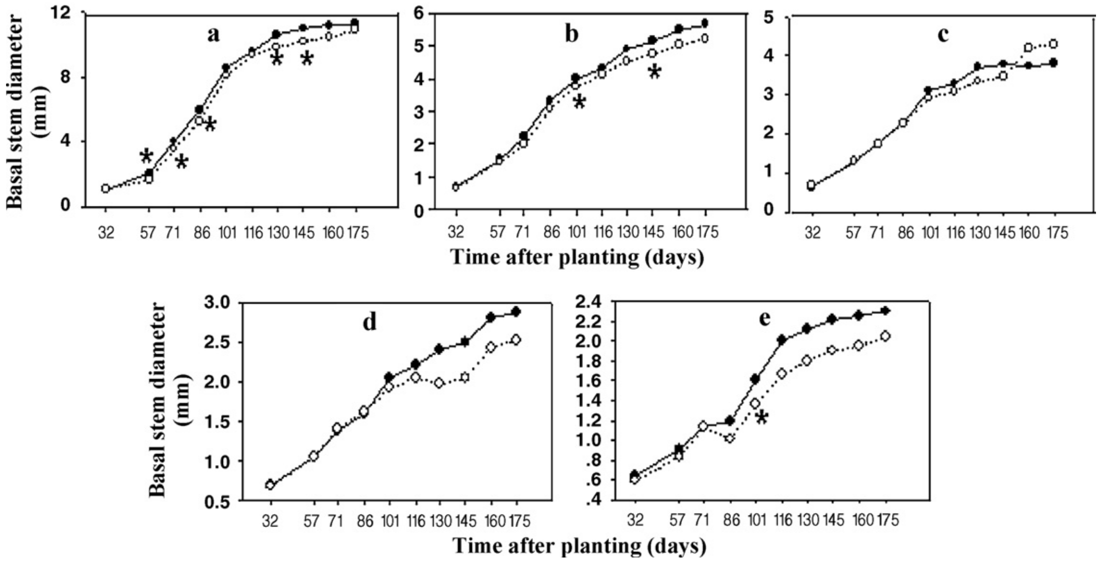

Fig. 6. Mean basal stem diameter of plants resulting from 3-year-old PSSB (◯) and freshly produced seeds (●) growing at different densities (a: 1 plant/pot; b: 13 plants/pot; c: 25 plants/pot; d: 85 plants/pot; e: 313 plants/pot) during the whole growing season. *Differences of mean basal stem diameter between plants resulting from 3-year aged seeds (PSSB) and plants resulting from new seeds significantly different at the same sampling time (*t*-test, $p < 0.05$).

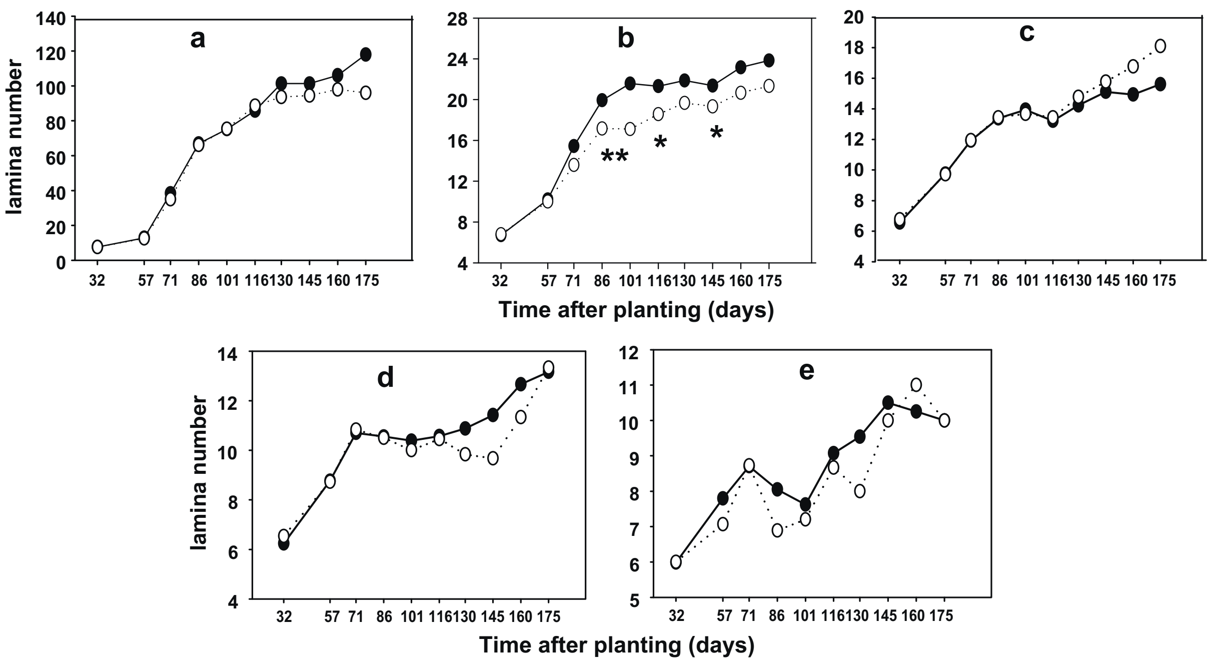

Fig. 7. Mean number of leaves of plants resulting from 3-year-old PSSB (◯) and from freshly produced seeds (●), respectively, at different densities (a: 1 plant/pot; b: 13 plants/pot; c: 25 plants/pot; d: 85 plants/pot; e: 313 plants/pot) during the whole growing season. *Mean number of leaves between plants resulting from 3-year aged seeds (PSSB) and from new seeds, respectively, significantly different at the same sampling time (*t*-test, $p < 0.05$).

Competition increased with increase in growing time and planting density (Fig. 3). As a result, average biomass, plant height, basal stem diameter and number of leaves of individual *E. adenophorum* plants decreased considerably with increase of planting density (Figs. 4–7). The longer the time after planting, the greater were the differences among different densities. By contrast, from 117 days after planting onwards the total biomass per pot did not differ significantly among densities of 13, 25, 85 and 313 per pot. This indicates that individuals of *E. adenophorum* suffered density-dependent reductions in growth rate and size. This simulates the competition situation individual plants are confronted with, which germinate in great amounts from PSSB 3-year seeds and from new seeds in the field.

However, there was no significant difference in competitive ability between plants germinated from 3-year-old PSSB seeds and from freshly produced seeds of *E. adenophorum*. When compared at a certain time during the 175-day growing period, differences in all the growth parameters and in biomass between the two plant cohorts were significant only at a very few sampling times. Under all competition densities, individual biomass, average height, basal stem diameter and leaf number of plants germinated from new seeds might be somewhat higher than that of plants from aged PSSB seeds, but these differences were seldom significant (Figs. 4–7). This suggests that *E. adenophorum* plants germinated from viable seeds in PSSB still maintain a certain level of competitive ability to their sibling neighborhood. This, on the other hand, indicates that the genetically fixed ability for an efficient use of resources still existed in the PSSB seeds. Bennington et al. (1991) compared plants of *Luzula parviflora* grown from old (197 ± 89 years) seeds buried by a solifluction lobe in Alaska and new seeds and found that plants developed from the new seeds were larger, had more leaves, grew better at high temperatures and were more sensitive to increased plant densities than those germinated from old seeds (McGraw et al., 1991). Other than in the present experiment, the old seeds and the new seeds were not from the same population. Another comparison of freshly produced diaspores and those stored dry for 4 years in the laboratory showed for *Bromus tectorum* contrasting vitality of the two seed sources. Delayed germination and lower biomass were observed with old seeds from a meadow population of the grass, whereas there was no delay in germination and no biomass difference of the resulting plants if old and new seeds were compared which were sampled from a sagebrush population of the species (Rice and Dyer, 2001).

PSSB was proposed to be important as a means ensuring continuation of a species at disturbed sites when mother plants died (Shen et al., 2003). Ellner (1986) and Cohen and Levin (1991) noted that PSSB was an effective bet-hedging strategy in variable or unpredictable environments that could buffer against years with reproductive failures, reducing the probability of local extinction. Long-term studies of population dynamics by Kalisz and McPeek (1992) revealed that PSSB can maintain population stability when the population growth rate is decreasing. PSSB also plays an important role in population variability and diversity. Epling et al. (1960) and Gottlieb (1974) found that a PSSB could retard genetic responses to new selection pressure because the population in any given year may be composed of individuals derived from seeds that matured over the past several years. Even after a “bad” year in which few seeds were produced, the allelic frequency of the offspring fluctuated within a very narrow amplitude, and rare alleles were not lost from this population. However, all of those functional roles for PSSB were deduced from the reality that seeds in PSSB could germinate several years after they mature. No direct evidence showed the capability of PSSB seeds in achieving these roles. Our result confirm that plant germinating from the PSSB of *E. adenophorum* still maintain a certain level of competiveness in low and in high competitive growth conditions against their siblings that resulted from new seeds of the same population. The survival rate of PSSB decreased greatly, but it did not significantly affect germination speed or competitive ability. Seeds stored in soil face a very high probability of death, but some can survive and these maintain a relative high fitness level in both the germination and plant growth stages. These findings provide a basal support for the function of the PSSB providing seed resources for the establishment of vital and competitive individuals of a species over the course of several years.

Eupatorium adenophorum is a worldwide noxious weed with high invasive ability. In southern China it has a very high seed density (2199 indiv./m^2) in the soil seed bank under various vegetation cover, and nearly half of the seeds (897 indiv./m^2) are located below soil surface (>2 cm depth: Shen et al., 2006). This means that a huge PSSB is formed. This high density of seeds will ensure a long occupation time of sites and maintain the possibility for invasion even in a bad seed production year. This result provides another clue explaining why this species has a high invasibility, making control and management of *E. adenophorum* very difficult.

Acknowledgements

This study was supported by “Light in Western China” Program of Chinese Academy of Sciences. We thank Professors Baskin for help with writing the manuscript.

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