*Seed Science Research* (2006) **16**, 157–162 DOI: 10.1079/SSR2006240

# Persistent soil seed banks of the globally significant invasive species, *Eupatorium adenophorum*, in Yunnan Province, south-western China

**Youxin Shen[1,2*], Wenyao Liu[1], Jerry M. Baskin[3], Carol C. Baskin[3,4] and Min Cao[1]**

[1]Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences (CAS), Kunming, 650223, P.R. China; [2]Graduate School, CAS, Beijing, 100039, P.R. China; [3]Department of Biology, University of Kentucky, Lexington, KY 40506-0225 USA; [4]Department of Plant and Soil Sciences, University of Kentucky, Lexington, KY 40546-0312 USA

## Abstract

Soil cores were collected at different times between the seed germination and dispersal seasons of *Eupatorium adenophorum* from 19 sites at five stations with different kinds of vegetation in Yunnan, south-western China. Mother plants of *E. adenophorum* were absent from eight of the sites, and their frequency was low at nine other sites. However, persistent soil seed banks were present at all 19 sites. Seed density in the 0–10 cm soil layer varied from 47 to 13,806 seeds $m^{-2}$, and averaged 2199 seeds $m^{-2}$. Fifty-seven percent of the seeds of *E. adenophorum* were in the 0–2 cm soil layer, 24% in the 2–5 cm layer and 19% in the 5–10 cm layer. The percentage of cores from which seedlings emerged ranged from 33–100% across all sites. Seed density and seedling emergence percentages varied significantly among the five stations, and both were positively correlated with abundance of mother plants.

**Keywords: *Eupatorium adenophorum*, invasive weeds, persistent soil seed bank, seedling emergence**

## Introduction

*Eupatorium adenophorum* Sprengel [syn. *Ageratina adenophora* (Sprengel) R. King & H. Robinson] (*Asteraceae*) is a noxious herbaceous perennial weed that reproduces by both seeds and vegetative means (Liu *et al.*, 1985). The species is native to central Mexico (Germplasm Resources Information Network, 2005), and it has been introduced into many other parts of the world, including Australia (Auld and Martin, 1975), Hawaii (Bess and Haramoto, 1959), India (Rahman and Agarwal, 1991), New Zealand (Hoy, 1960), South Africa (Kluge, 1991), mainland USA (Fuller, 1981) and many Asian countries (Andrews and Falvey, 1979). The first record of this species in China was made in the 1940s, in Yunnan Province, and thus it is presumed to have entered China across the Sino-Burma (now Myanmar) border (Liu *et al.*, 1985). During the past 60 years, huge areas in southern China have been invaded by this species. For example, 247,726 $km^2$ of land are infested in Yunnan (Zhao and Ma, 1989) and 3751 $km^2$ in Sichuan (Zhou and Xie, 1999). In the infested areas, *E. adenophorum* has invaded agricultural land, forests and pastures, and caused huge economic losses (Zhao and Ma, 1989; Zhou and Xie, 1999). Unfortunately, methods to control its spread in China have not been successful, and the infested area has expanded north and east at a rate of 20 (Zhou and Xie, 1999) to 60 km $yr^{-1}$(Xiang, 1991).

Some species form a persistent soil seed bank (PSB) in which seeds produced in a given year remain viable in the habitat for 1 year or longer (Thompson and Grime, 1979; Walck *et al.*, 2005). A PSB is an adaptation to temporal and spatial variation in the environment, thus increasing establishment success and reducing the chance of extinction (Baskin and Baskin, 1989; Thompson, 2000). Species with a small seed mass and a small surface/volume ratio tend to develop a PSB (Thompson *et al.*, 1993; Bekker *et al.*, 1998). *E. adenophorum* seeds are very small, and they are wind dispersed, which ensures their wide and rapid spread (Auld and Martin, 1975; Liu *et al.*, 1989). Seed production of *E. adenophorum* is very high (up to 260,000–280,000 $m^{-2}$ $yr^{-1}$), and the species has been

*Correspondence:
Fax: +86 871 5160916
E-mail: yxshen@xtbg.ac.cn

reported to form a large soil seed bank (Liu *et al.*, 1989). However, Liu *et al.* (1989) collected soil samples from only one site, and they did not distinguish between transient and persistent seed banks.

The purpose of our study was to determine if *E. adenophorum* has a PSB, and if so, to quantify its size and distribution in various habitats in southern China, with and without mother plants in the above-ground vegetation. Thus, we collected soil samples between the seed germination and dispersal seasons from 19 sites at five stations in Yunnan Province, the most infested area in China, and used the seedling emergence method to determine number and vertical distribution of *E. adenophorum* seeds in the soil seed bank.

## Materials and methods

This study was carried out in Yunnan Province, People's Republic of China, where *E. adenophorum* is a noxious weed over a large area. Yunnan (21°8′32″–29°15′8″N; 97°31′39″–106°11′47″E) is a mountainous province in SW China with a diversity of geographical features and environmental conditions. Altitude ranges from 6740 m above sea level, in the north-west part of the province, to 75 m in the south-east. Huge environmental differences occur in temperature and rainfall from the base to the top of mountains, some of which are covered with permanent ice. The valleys are hot and dry. Various types of karst occur in the eastern part of the province.

Five stations (SB1–SB5) and a total of 19 sites within them were chosen, based on differences in physical habitat, secondary or planted vegetation type and/or abundance (including 0) of mother plants of *E. adenophorum* in the above-ground vegetation (Fig. 1, Tables 1, 2). SB5 is outside the normal distribution range of *E. adenophorum* in Yunnan, and the other four sites are within it (Zhao and Ma, 1989). At SB1, SB2 and SB3, vegetation was natural (successional), and at SB4 and SB5 forests and shrubs were planted. Eighteen of the 19 sites chosen for sampling at the five stations were covered by trees, shrubs or grasses, and one site was a new, unvegetated landslide. The forests, whether natural or planted, were highly fragmented and surrounded by shrublands and grasslands. Sites within the stations were separated by distances of about 500–1000 m. Two to three plots (each 20 m × 20 m) were established at the 13 forest and shrub sites and 2–3 plots (each 10 m × 10 m) at the five grassland sites and the one landslide site. Plots within the sites were chosen randomly and were 10–20 m apart. Within each plot, coverage of plants of *E. adenophorum* was estimated visually.

Five soil cores (each 10 cm × 10 cm) were taken from each plot, for a total of 10–15 cores per site. Thus, 30 cores each (3 sites × 10 cores per site) were taken at SB1, SB2 and SB3, 90 cores (6 sites × 15 cores per site) at SB4 and 60 cores (4 sites × 15 cores per site) at SB5. Seeds of *E. adenophorum* mature in April and germinate in May and June in most parts of Yunnan (Liu *et al.*, 1989). Soil samples were taken in August 2001 at SB4 and in March 2002 at SB1, SB2, SB3 and SB5. Each soil core was divided into three depth layers, viz. 0–2, 2–5 and 5–10 cm, except those at station SB5, where the soil contained a large quantity of coarse rock materials, making separation into layers impossible. At the site covered with pine forest (station SB4), the litter layer was thick; thus, it was treated as a separate layer. At the other stations, where the litter layer was thin, it was included in the 0–2 cm soil layer.

Each soil sample was washed through a 4-mm-mesh sieve to eliminate course materials, and then

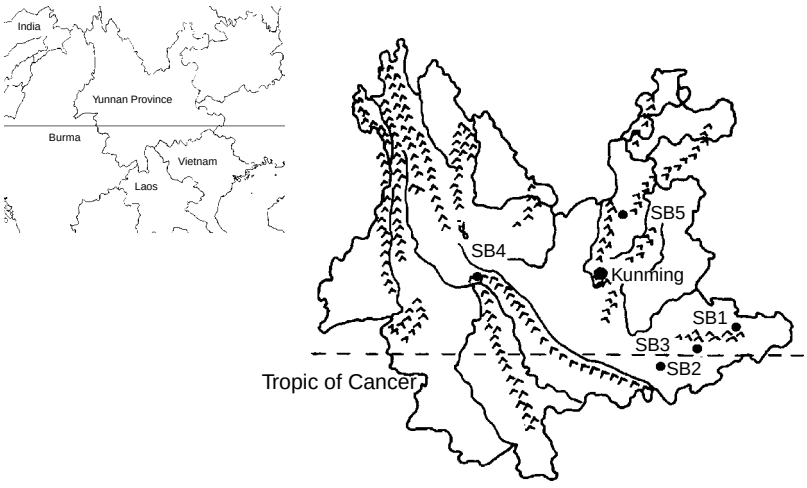


**Figure 1.** Geography and topography of Yunnan Province, showing locations of the five seed-bank sampling stations (SB1–SB5).

https://doi.org/10.1079/SSR2006240 Published online by Cambridge University Press

**Table 1.** Geographical location, physical environmental characteristics and forest status of the five *Eupatorium adenophorum* seed-bank collection stations in Yunnan Province, SW China

| Station | SB1 | SB2 | SB3 | SB4 | SB5 |
|---|---|---|---|---|---|
| Latitude | 23°59′N | 23°16′N | 23°26′N | 24°54′N | 26°15′N |
| Longitude | 104°58′E | 104°24′E | 104°39′E | 100°30′E | 103°10′E |
| Altitude (m) | 1100–1150 | 1450–1500 | 1450–1500 | 1400–1500 | 1400–1500 |
| Geographical feature | Karst upland | Karst upland | Karst upland | Hot and dry valley | Hot and dry valley |
| Average annual temperature (°C) | 16.6 | 17.8 | 15.8 | 18.7 | 20 |
| Average annual rainfall (mm) | 1071 | 1000 | 1294 | 700 | 693 |
| Slope (degrees) | 20–40 | 20–40 | 20–40 | 10–30 | 30–40 |
| Rock surface (%) | 60–70 | 60–70 | 60–70 | 0 | 0 |
| Forest status | Regenerated in 1980s | Regenerated in 1980s | Regenerated in 1980s | Planted in 1990s | Planted in 1990s |

through a 0.21-mm-mesh sieve to eliminate fine materials (Ter Heerdt *et al.*, 1996). The concentrated residue, which contained all seeds from the sample, was spread out evenly on to a 3 cm layer of perlite in plastic seed trays (*c.* 18 cm × 10 cm × 10 cm deep). To check for contamination, 12 trays with sterilized soil were placed randomly in a non-heated greenhouse in Kunming, and seedling emergence monitored. All trays were monitored and watered, usually twice a day. Seedlings were counted and discarded as soon as they could be identified, or they were transplanted into 15-cm-diameter pots filled with fertile soil, and grown until identification was possible. Soil in the trays was stirred 2–3 times during the germination monitoring period, normally after a large flush of germination. All germination trials were terminated in October 2002, seven (SB1, SB2, SB3 and SB5) and 14 (SB4) months after the soil samples were collected.

Seed density (seeds $m^{-2}$) of *E. adenophorum* and total seed density for all species germinated in the trays were calculated for each site. The percentage of cores from which seedlings of *E. adenophorum* emerged and percentage of seeds of this species in the total seed density of a site were calculated. *E. adenophorum* seeds did not emerge from all soil cores taken at a site. No seeds of any species germinated in the trays used to monitor contamination. Significant differences ($P < 0.05$) in mean seed-bank density and its percentage in each depth layer between sites were tested using one-way analysis of variance (ANOVA) for each station, and multiple comparisons were performed by Fisher's LSD range test. Prior to analysis, density data were logarithmically transformed. One-way ANOVA also was applied to test significant differences ($P < 0.05$) in seed-bank densities and seedling emergence percentages between stations. Correlation analysis with a two-tailed significance test was used to evaluate the relationship between coverage of mother plants and seed density; between coverage of mother plants and seedling emergence percentage; and between coverage of mother plants and percentage of seeds of *E. adenophorum* in the 0–2 and 2–5 cm soil-depth layers at SB4.

## Results

Persistent seed banks of *E. adenophorum* occurred at all 19 sites at the five stations (Table 2). Among the 19 sites, the percentage of soil cores from which seedlings of *E. adenophorum* emerged ranged from 33 to 100% and averaged 76%. Mean seed density (seeds $m^{-2}$) among the five stations ranged from 72 (SB5) to 5191 (SB4). Among the 19 sites, mean seed density of *E. adenophorum* in the soil ranged from 47 to 13,806 seeds $m^{-2}$ and averaged 2199 $m^{-2}$. Seeds of *E. adenophorum* accounted for 0.5–22.2% of the total seed density at a site, with an average of 9.4% for all sites. With some exceptions at SB4, seed density of *E. adenophorum* in the PSB was higher at forest sites than at shrub and grassland sites. Plants of *E. adenophorum* did not occur at eight of the sites and had low occurrence at nine sites. Thus, there were only two sites at which plants of this species had high occurrence, i.e. SB4 pine forest and SB4 shrub.

Mean seed density ($F = 5.25$, $P = 0.009$) and the percentage of soil cores from which seedlings emerged ($F = 9.05$, $P = 0.01$) differed greatly among the five stations. Significant differences were found between: (1) secondary forest and shrub at SB3; (2) secondary forest and grass at SB3; and (3) most sites at SB4 (Table 2). Although mother plants did not occur at SB1 or SB5, seeds of *E. adenophorum* were present: 160–570 $m^{-2}$ at SB1 and 47–93 $m^{-2}$ at SB5. Mother plants also were not present at the SB2 secondary forest site, where seed density was 2060 $m^{-2}$ (Table 2). Generally, there was a trend in seed density increase with an increase in mother plant cover for the 19 sites. Mean density of seeds in the soil seed bank ($r = 0.6213$,

https://doi.org/10.1079/SSR2006240 Published online by Cambridge University Press

**Table 2.** Coverage of mother plants, percentage of soil cores from which *Eupatorium adenophorum* (*E.a.*) seedlings emerged, seed density of *E. adenophorum* and percentage of the total soil seed-bank density accounted for by seeds of *E. adenophorum* across different vegetation types at 19 sites at five sampling stations. Numbers with the same letter in the seed-density column do not differ significantly in seed density at the same station

| Station/site | Vegetation type | Coverage of mother plants (%) | Percentage of cores from which seedlings of *E.a.* emerged | Seed density of *E.a.* ($m^{-2}$) (mean ± SE) | *E.a.* seeds as percent of total seed density |
|---|---|---|---|---|---|
| SB1 | Secondary forest | 0.0 | 80 | 570 ± 177a | 12.6 |
| SB1 | Shrub | 0.0 | 80 | 500 ± 134a | 12.2 |
| SB1 | Grass | 0.0 | 60 | 160 ± 52a | 2.2 |
| SB2 | Secondary forest | 0.0 | 100 | 2060 ± 348a | 17.2 |
| SB2 | Shrub | 2.0 | 80 | 1160 ± 391a | 10.6 |
| SB2 | Grass | 2.0 | 90 | 1380 ± 486a | 20.3 |
| SB3 | Secondary forest | 2.0 | 90 | 3310 ± 1391a | 22.2 |
| SB3 | Shrub | 2.0 | 90 | 770 ± 148b | 19.7 |
| SB3 | Grass | 2.0 | 70 | 440 ± 152b | 7.8 |
| SB4 | Pine forest | 38.0 | 100 | 13 806 ± 1499a | 3.3 |
| SB4 | Shrub | 87.0 | 100 | 9247 ± 1759b | 3.9 |
| SB4 | *Acacia* forest | 3.0 | 93 | 5673 ± 1285c | 4.8 |
| SB4 | Grass | 3.0 | 93 | 1940 ± 1163d | 3.9 |
| SB4 | *Eucalyptus* forest | 2.0 | 73 | 333 ± 86e | 0.7 |
| SB4 | *Leucaena* forest | 2.0 | 67 | 147 ± 51e | 0.5 |
| SB5 | *Leucaena* forest | 0.0 | 40 | 93 ± 34a | 6.7 |
| SB5 | Shrub | 0.0 | 33 | 66 ± 22a | 8.2 |
| SB5 | Grass | 0.0 | 53 | 83 ± 23a | 6.8 |
| SB5 | New landslide material | 0.0 | 60 | 47 ± 22a | 16.0 |
| Average | | | 76 | 2199 ± 838 | 9.4 |

$P = 0.006$) and percentage of soil cores from which seedlings of *E. adenophorum* emerged ($r = 0.4794$, $P = 0.044$) were positively correlated with cover of mother plants.

At most sites, seed density decreased with soil depth (Table 3). Seeds in the 0–2 cm layer accounted for 23.8–90.6% of total seeds across the 15 sites (average 57.5%; SB1, SB2, SB3, SB4), those from the 2–5 cm layer for 6.4–45.7% (average 23.8%) and those from the 5–10 cm layer for 0–46.2% (average 18.7%). Percentage of seeds in a vertical layer of soil differed significantly among different sites only for the 0–2 cm ($F = 2.45$, $P = 0.04$) and 2–5 cm ($F = 3.39$, $P = 0.008$) layers at SB4. Correlation between coverage of mother plants and seed percentage was not significant, either for layer 0–2 cm or layer 2–5 cm.

## Discussion

Seeds of *E. adenophorum* mature and are dispersed in April in southern China, and they germinate mainly in May and June, at the beginning of the rainy season (Liu *et al.*, 1989). Our soil samples were collected after the previous germination season and before the next dispersal season. As such, seeds in the samples were not from a transient seed bank (Thompson and Grime, 1979; Walck *et al.*, 2005). That this species can form a persistent seed bank is shown by the presence of seeds in the 2–5 cm and 5–10 cm layers at SB1, where mother plants were absent (Table 3), and clearly indicates that they are not recent arrivals to the site (Thompson *et al.*, 1997). The only previous seed-bank study on *E. adenophorum* known to us is one in which number and vertical distribution of seeds in soil was evaluated in central Yunnan (Liu *et al.*, 1989).

**Table 3.** Percentages of *Eupatorium adenophorum* seeds in three soil-depth layers of different vegetation types at research stations SB1–SB4 in Yunnan Province, SW China. Numbers for a soil-depth layer at SB4 with the same letter do not differ significantly

| Station | Vegetation type | 0–2 cm | 2–5 cm | 5–10 cm |
|---|---|---|---|---|
| SB1 | Secondary forest | 41.3 | 45.7 | 13.0 |
| | Shrub | 28.5 | 34.6 | 36.9 |
| | Grass | 23.8 | 33.3 | 42.9 |
| SB2 | Secondary forest | 34.6 | 19.2 | 46.2 |
| | Shrub | 58.6 | 30.2 | 11.2 |
| | Grass | 53.8 | 25.5 | 20.7 |
| SB3 | Secondary forest | 52.0 | 20.3 | 27.8 |
| | Shrub | 30.4 | 30.7 | 39.0 |
| | Grass | 54.0 | 25.8 | 20.2 |
| SB4 | Pine forest | 90.6a | 6.4b | 3.0 |
| | Shrub | 88.6a | 7.5b | 3.8 |
| | *Leucaena* forest | 67.7c | 29.1a | 3.3 |
| | *Acacia* forest | 81.3abc | 11.2b | 7.5 |
| | *Eucalyptus* forest | 86.7ab | 8.4b | 4.9 |
| | Grass | 70.9bc | 29.1a | 0.0 |
| Average | | 57.5 | 23.8 | 18.7 |

https://doi.org/10.1079/SSR2006240 Published online by Cambridge University Press

However, in that study soil samples were collected immediately after seed dispersal, and as such, transient and persistent (if present) seed banks could not be distinguished. Thus, our study appears to be the first one to demonstrate that *E. adenophorum* can form a persistent seed bank.

The presence of soil seed banks at SB1 and SB5 (Table 2), where mother plants were absent, might indicate long-distance dispersal, since seeds of *E. adenophorum* are windborne (Auld and Martin, 1975; Liu *et al*., 1989). An alternative explanation is that the presence of seed banks at these two sites is evidence that the species grew there once, but does so no longer. The fact that 59–77% of the seeds in the PSB at SB1 were in the 2–5 cm and 5–10 cm layers (Table 3) suggests that they are not recent arrivals to the site (Thompson *et al*., 1997). Thus, they may be relics of the former presence of mother plants of *E. adenophorum* at SB1. Since soil cores collected at SB5 could not be divided into layers (see Methods), depth distribution of seeds from this station could not be determined. Neither the reason(s) for absence of mother plants of *E. adenophorum* at these two sites, even though seed banks were present, nor how long they had been absent from them, is known.

The rainy season (May–October) begins immediately after *E. adenophorum* seeds are dispersed (Xu, 1991). Burial of seeds in soil before they germinate and prevention of germination during the rainy season of at least a portion of the seeds are prerequisites for persistence of *E. adenophorum* seeds in soil. Further, seeds of *E. adenophorum* require light to germinate (Auld and Martin, 1975; Auld, 1981), and light filtered through a plant canopy inhibits germination of many weeds (Fenner, 1980), i.e. because of the high far-red/red photon irradiance in leaf-filtered sunlight, which can differ among species (Baskin and Baskin, 1998). In our study area, forest is the dominant zonal vegetation, and shrubland and grassland occur on degraded land (Wu, 1987). The highest seed-bank density was found in the pine forest site at SB4 (13,806 seeds $m^{-2}$), which was 2.4 (*Acacia* forest, SB4) to 148.5 (*Leucaena* forest, SB5) times that at the other sites covered with tree vegetation. This may be caused by the difference in the litter layer, since seeds of *E. adenophorum* penetrate pine needles more easily than they do leaves of broad-leaved trees (Y. Shen, personal observation, 2004).

In agriculture, forest and pasture land, mother plants of *E. adenophorum* may be eliminated in a particular year and, thus, *in situ* seed production is interrupted. However, existence of a PSB and wind transport of seeds from short and long distances will make it likely that germination will occur in the system the next year. Further, seeds buried in the top 10 cm of soil may be brought to the surface via soil disturbance by humans and/or livestock, resulting in a new peak of germination. Thus, a management plan for *E. adenophorum* should include the seed-bank biology of this species. A critical question that remains to be answered about *E. adenophorum* is how long can the seeds remain viable in the soil?

## Acknowledgements

We thank Professor Liu Lunhui, a retired *E. adenophorum* specialist, for help with research activities. This study was supported by China's National Key Project for Basic Research on Ecosystem Changes in Longitudinal Range-Gorge Region and Trans-boundary Eco-security of Southwest China (No. 2003CB415101) and by the fund for Top One Hundred Young Scientists, CAS (BRJH 2002098).

## References

**Andrews, A.C. and Falvey, L.** (1979) The ecology of *Eupatorium adenophorum* in native and improved pastures in the northern Thailand highland. pp. 351–353 *in* Delfosse, E.S. (Ed.) *Proceedings of the 6th Asian-Pacific weed science society conference*. Sydney, Australia.

**Auld, B.A.** (1981) Invasive capability of *Eupatorium adenophorum*. pp. 145–147 *in* Venkata Rao, B.V. (Ed.) *Proceedings of the 8th Asian-Pacific weed science society conference*. Bangalore, India.

**Auld, B.A. and Martin, P.M.** (1975) Autecology of *Eupatorium adenophorum* in Australia. *Weed Research* **15**, 27–31.

**Baskin, C.C. and Baskin, J.M.** (1998) *Seeds: Ecology, biogeography, and evolution of dormancy and germination*. San Diego, Academic Press.

**Baskin, J.M. and Baskin, C.C.** (1989) Physiology of dormancy and germination in relation to seed bank ecology. pp. 53–66 *in* Leck, M.A.; Parker, V.T.; Simpson, R.L. (Eds) *Ecology of soil seed banks*. San Diego, Academic Press.

**Bekker, R.M., Bakker, J.P., Grandin, U., Kalamees, R., Milberg, P., Poschlod, P., Thompson, K. and Willems, J.H.** (1998) Seed size, shape and vertical distribution in the soil: indicators of seed longevity. *Functional Ecology* **12**, 834–842.

**Bess, H.A. and Haramoto, F.H.** (1959) Biological control of pamakani, *Eupatorium adenophorum*, in Hawaii by a tephritid gall fly, *Procecidochares utilis*. 2. Population studies of the weed, the fly, and the parasites of the fly. *Ecology* **40**, 244–249.

**Fenner, M.** (1980) Germination tests on thirty-two East African weed species. *Weed Research* **20**, 135–138.

**Fuller, T.C.** (1981) Introduction and spread of *Eupatorium adenophorum* in California. pp. 277–280 *in* Venkata Rao, B.V. (Ed.) *Proceedings of the 8th Asian-Pacific weed science society conference*. Bangalore, India.

**Germplasm Resources Information Network (GRIN)** USDA, ARS, National Genetic Resources Program, National Germplasm Resources Laboratory, Beltsville, Maryland, [online database]: http://www.ars-grin.

gov2/cgi-bin/npgs/html/taxon.pl?316409 (accessed 19 December 2005).

**Hoy, J.M.** (1960) Establishment of *Procecidochares utilis* Stone on *Eupatorium adenophorum* Spreng. in New Zealand. *New Zealand Journal of Science* **102**, 159–161.

**Kluge, R.L.** (1991) Biological control of crofton weed, *Ageratina adenophora* (Asteraceae), in South Africa. *Agriculture, Ecosystems and Environment* **37**, 187–191.

**Liu, L.H., Liu, W.Y., Zhen, Z. and Jing, G.F.** (1989) The characteristic research of autecology of Pamakani (*Eupatorium adenophorum*). *Acta Ecologica Sinica* **9**, 66–70 (in Chinese with English abstract).

**Liu, L.H., Xie, S.C. and Zhang, J.H.** (1985) Distribution, harmfulness of Pamakani (*Eupatorium adenophorum*) and discussion on the prevention strategies. *Acta Ecologica Sinica* **5**, 1–6 (in Chinese with English abstract).

**Rahman, O. and Agarwal, M.L.** (1991) Biological control of crofton weed (*Eupatorium adenophorum* Spreng.) by a fruit fly *Procecidochares utilis* Stone in eastern Himalayas. *Indian Journal of Weed Sciences* **22**, 98–101.

**Ter Heerdt, G.N.J., Verweij, G.L., Bekker, R.M. and Bakker, J.P.** (1996) An improved method for seed bank analysis: seedling emergence after removing the soil by sieving. *Functional Ecology* **10**, 144–151.

**Thompson, K.** (2000) The functional ecology of soil seed banks. pp. 215–235 *in* Fenner, M. (Ed.) *Seeds: The ecology of regeneration in plant communities* (2nd edition). Wallingford, CAB International.

**Thompson, K., Bakker, J.P. and Bekker, R.M.** (1997) *The soil seed banks of north west Europe: Methodology, density and longevity.* Cambridge, Cambridge University Press.

**Thompson, K., Band, S.R. and Hodgson, J.G.** (1993) Seed size and shape predict persistence in the soil. *Functional Ecology* **7**, 236–241.

**Thompson, K. and Grime, J.P.** (1979) Seasonal variation in the seed banks of herbaceous species in ten contrasting habitats. *Journal of Ecology* **67**, 893–921.

**Walck, J.L., Baskin, J.M., Baskin, C.C. and Hidayati, S.N.** (2005) Defining transient and persistent seed banks in species with pronounced seasonal dormancy and germination patterns. *Seed Science Research* **15**, 189–196.

**Wu, Z.Y.** (1987) *Vegetation of Yunnan* (in Chinese). (Chinese) Science Press, Beijing.

**Xiang, Y.X.** (1991) Distribution and harmfulness of *Eupatorium adenophorum* and its control. *Chinese Journal of Weed Science* **5**(4), 10–11 (in Chinese with English abstract).

**Xu, Y.H.** (1991) *Climate of South-West China* (in Chinese). Beijing, P.R. China, Meteorological Press.

**Zhao, G.J. and Ma, Y.P.** (1989) Investigation of the distribution and harmfulness of Pamakani (*Eupatorium adenophorum*) in Yunnan. *Chinese Journal of Weed Science* **3**(2), 37–40 (in Chinese with English abstract).

**Zhou, S. and Xie, Y.L.** (1999) The investigation report on the poisonous and injurious plant – *Eupatorium adenophorum* Spreng. in Sichuan Province. *Sichuan Grassland* **1999**(2), 39–42 (in Chinese with English abstract).

Received 26 October 2005
accepted after revision 14 February 2006