Variation in reproductive characteristics of *Eupatorium adenophorum* populations in different habitats

X-J YU* & K-P MA*

*Laboratory of Quantitative Vegetation Ecology, Institute of Botany, Chinese Academy of Sciences, Beijing, China, and †College of Forestry, Beihua University, Jilin, China

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Summary

The invasive plant, *Eupatorium adenophorum*, produces large numbers of small seeds with a high germination rate. However, this investigation showed that *E. adenophorum* populations in an evergreen broad-leaved forest had a high proportion of seedlings when compared with clonal plants. Whereas an opposite pattern was found in a deciduous broad-leaved forest and in a roadside site. A seed addition experiment where *E. adenophorum* seeds were added to each of the three habitats did not increase the number of *E. adenophorum* seedlings at any of the three field sites. Field and greenhouse experiments demonstrated that a soil litter layer significantly reduced the number of *E. adenophorum* seedlings during the early seedling emergence period. However, at later periods, the litter cover did not affect survival and growth of individuals. The emergence of *E. adenophorum* seedlings was significantly increased in field experiments when there was no litter, and parental plants were removed. Finally, the growth of seedlings was significantly reduced when planted with their parental plants in a root box experiment. In the low-resource environment of the evergreen broad-leaved forest, *E. adenophorum* reproduced primarily by its abundant seed production. In the more open deciduous broad-leaved forest and roadside site, the populations reproduce primarily by vegetative clones that can grow quickly, are better competitors and could take advantage of the high-resource environment.

Keywords: exotic species, invasion, reproduction, seed production, seedling, clonal plant.

**Introduction**

The weedy perennial shrub, crofton weed (*Eupatorium adenophorum* Spreng.), is native to Central America. However, it is presently a serious weed in Australia, New Zealand, India, Thailand, Sri Lanka, the Canary Islands, Jamaica, Fiji, South Africa, the United States and China. In these regions, it has become a serious invader in croplands, grasslands and forests and has the ability to reduce agricultural production, impact natural ecosystem function and can evade easy control measures [Auld, 1970; Andrews & Falvey, 1979; Verma & Minhas, 1988; Morris, 1989; Zhao & Ma, 1989]. The weed came to China from Burma half a century ago but recently has been aggressively colonising the mountainous areas in southwestern China. In a recent survey, this weed was described as the most common weed in agricultural and natural ecosystems in these regions (Xiang, 1991; Li, 1998; Ding, 2002).

The ability for *E. adenophorum* to spread from its original habitat to invaded habitats or from old invaded habitats to new habitats is explained largely by its high seed production with high germination rates in most sites [White, 1944; Auld, 1970; Andrews & Falvey, 1979; Auld, 1981; Zhao & Ma, 1989; Xiang, 1991; Fromont & King, 1992; McKellar, 1999; Helen, 2003; State of Queensland (Department of Natural Resources and Mines), 2004]. However, little is known about reproduction of the plant after it invades a new habitat or ecosystem.

**Correspondence:** K-P Ma, Laboratory of Quantitative Vegetation Ecology, Institute of Botany, Chinese Academy of Sciences, Beijing 100093, China.
Tel: (+86) 10 68236223; Fax: (+86) 10 82599518; E-mail: kpma@ibcas.ac.cn

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In the field, we found that populations of *E. adenophorum* in open deciduous broad-leaved forests and roadside habitats comprised few seedlings but populations in closed evergreen broad-leaved forests had many seedlings. Differences in seed production could not explain this observation. Why were fewer seedlings present in the deciduous broad-leaved forest and roadside sites where *E. adenophorum* was a dominant plant when compared with the other sites with more seedlings but a sparser adult population? Do the populations reproduce by other mechanisms, such as cloning, at those sites?

In many studies, *E. adenophorum* has been reported to depend on a high-light environment (Auld, 1981; Tripathi & Yadav, 1982; Fromont & King, 1992; Sun et al., 1992), and different light conditions have been used to explain differences in invasion success in various habitats. However, different light conditions may not explain the reproductive characteristics of *E. adenophorum* populations in different habitats.

In this study, we sought to understand the reproductive strategies of *E. adenophorum* by investigating the population structure of *E. adenophorum* in different sites, and conducting field and greenhouse experiments to explore how different factors, including seed resources, the soil litter layer and neighbouring parent plants, influence seedling emergence and growth. Understanding the conditions that affect the ability for this invasive plant to establish in different habitats can aid in the development of control strategies to ultimately prevent its spread.

**Materials and methods**

**Field sites**

Three sites were selected in southwestern China to investigate the reproductive characteristics of *E. adenophorum* in the field. All study sites were in the Hengduan Mountain range, which is characterised by a subtropical hot and arid valley climate with strong wet and dry seasons. Annual mean temperature ranges between 19.0°C and 21.0°C and annual precipitation between 760 and 1200 mm, which falls mainly during the rainy season (June to October). Evergreen broad-leaved forests were the dominant vegetation until 20–30 years ago, when logging and grazing activities reduced their distribution. Both deciduous broad-leaved and conifer forests (*Pinus yunnanensis* is dominant) are increasing in dominance. *Eupatorium adenophorum* began to invade this region approximately 15–20 years ago.

Three field sites were selected: an evergreen broad-leaved forest, a deciduous broad-leaved forest and along a roadside, all of which that had similar altitude, topography, gradient and soil types. At each site, 20 m × 30 m study plots were established. Site I, an evergreen broad-leaved forest, has been only lightly disturbed by human activities. The community structure was characterised by a dense forest canopy and a subcanopy layer dominated by natural vegetation and a low density of *E. adenophorum*. Site II, a deciduous broad-leaved forest, has been heavily disturbed by human activities, such as logging and grazing, and had an open forest canopy, little natural subcanopy vegetation and a dense population of *E. adenophorum*. Site III was along the roadside and has had frequent anthropogenic disturbance, little natural subcanopy vegetation, no trees or shrubs, and a very high density of *E. adenophorum* (Table 1). We believe that the three sites were invaded at nearly the same time due to their close proximity.

**Origin of Eupatorium adenophorum**

The origin of each *E. adenophorum* individual was determined by investigating its root characteristics, because cloned individuals remain attached to their mother plant before becoming a separate adult plant. The mother plant dies when the new plant matures, leaving a portion of the mother plant stem preserved at the joint of root and stem of the adult clonal individual. However, seedlings lack this vestigial clonal tissue of the mother plant.

In May 2003, we established fifteen 1 m × 1 m sample quadrats in each of the three sites, carefully excavated all *E. adenophorum* individuals in each quadrat, then separated each individual carefully, investigated the root characteristics and deduced the origin of each *E. adenophorum* individuals.

**Field experiment**

A potential limiting factor of reproduction by seed in *E. adenophorum* populations is the availability of seed sources. To test this, *E. adenophorum* seeds were added to six replicated 1 m × 1 m quadrats that were spaced evenly along a diagonal at each of the three sites at a density of 0.4 g m⁻² in May 2003 (hereafter called ‘S+’). Seeds were collected from the roadside sites close to experimental sites in April 2003. The seeds had an average weight of 0.0425 g/1 000 seeds and a germination rate of 92.5%, as determined in the laboratory. Six control quadrats were established at each of the three sites adjacent to the experimental quadrats with an identical arrangement along another diagonal.

In addition, another 12 quadrats (1 m × 1 m) were established in Site II, the deciduous broad-leaved forest.
Six of these quadrats were spaced evenly along the transverse midline, and another six of these quadrats were spaced evenly along the vertical midline at the site. In the former six quadrats at transverse midline, seeds were added without litter on the surface (S+ L−), and, in the latter six quadrats at vertical midline, seeds were added without litter and mature *E. adenophorum* plants were removed (S+ L− P−). The treatment period and quantity of seeds added to the quadrats were identical to those in the previous experiment. Every treatment was observed for 1 year, starting in July 2003, and the number *E. adenophorum* seedlings in each quadrant were noted every 2 months.

**Pot experiment**

The effect of soil litter on the emergence and growth of seedlings was investigated by adding seeds to 12 plastic pots (22 cm top diameter, 15 cm bottom diameter, 25 cm high) filled with natural soil from a deciduous broad-leaved forest in June 2003. A 2 cm thick litter layer was added to half the pots (*n* = 6) and seeds were added at a density of 30 seeds per pot. Litter material, which consisted mainly of dry leaves, was collected from a deciduous broad-leaved forest. In early July, the number of seedlings in each pot was recorded and four average-sized *E. adenophorum* individuals were selected.
and kept in each pot while the other seedlings were removed. All pots were placed in a plastic glasshouse and provided with plentiful quantities of distilled water once every 2 days. Seedlings were harvested in September 2003 and stem height, root length and fresh weight of each seedling were measured. Two plants were randomly chosen from each pot and dried for 24 h at 80°C in a drying oven to determine moisture content of fresh plants and to estimate the total dry biomass in each root box.

**Data analysis**

Data for all experiments were normally distributed. One-way analyses of variance (ANOVA, SPSS 10.0) were used to examine the significance of differences in the means between treatments.

**Results**

**Seedling and clonal composition of Eupatorium adenophorum populations at different sites**

The three populations exhibited varying proportions of seedlings and clonal plants. The proportion of seedlings under the evergreen broad-leaved forest was the highest, accounting for 60% of the total abundance of *E. adenophorum* (Fig. 1). The proportion of seedlings in the deciduous broad-leaved forest and roadside was less, each accounting for only 15% of the total abundance of *E. adenophorum*.

**Addition of Eupatorium adenophorum seed in different sites**

The number of newly emerged *E. adenophorum* seedlings was not significantly different among sites during the initial growth period (July 2003) when compared with the control treatments (*P > 0.05*). However, with time, differences in the abundance of newly emerged seedlings at the different sites became evident (Fig. 2). For example, the abundance of newly emerged seedlings
under the evergreen broad-leaved forest was about 6–10 times greater than under the deciduous broad-leaved forest or roadside site by the end of the study period in May 2004. In the seed addition treatment, the number of newly emerged *E. adenophorum* seedlings in each site was not significantly different from the controls at any time (from July 2003 to May 2004, $P > 0.05$).

**Effect of litter on the emergence of *Eupatorium adenophorum***

In July 2003, the number of newly emerged *E. adenophorum* seedlings in the ‘S+ L−’ treatment increased by 95–130% compared with the controls, and was significantly greater than both the ‘S+’ and control treatments ($P < 0.01$). However, in May 2004, the number of *E. adenophorum* seedlings in ‘S+ L−’ was not different to both the ‘S+’ and control treatments ($P > 0.05$) (Fig. 3).

**Effect of litter on establishment and growth of *Eupatorium adenophorum* seedlings in the pot experiment**

The pot experiment showed that litter significantly reduced the establishment of newly emerged *E. adenophorum* seedlings with 80% less emergence when compared with the no-litter treatment (one-way ANOVA; $F_{1,11} = 12.698$, $P < 0.01$) (Fig. 4). The individual biomass in the litter treatment did not differ from the control (one-way ANOVA; $F_{1,47} = 0.171$, $P > 0.05$).

**Effect of parental presence on *Eupatorium adenophorum* reproduction**

The number of newly emerged *E. adenophorum* seedlings in the ‘S+ L− P−’ treatment was double that of the treatments with parental plants and was significantly greater than the ‘S+ L−’ treatments ($P < 0.01$), control treatments ($P < 0.01$) and the ‘S+’ treatment ($P < 0.05$) (Fig. 5). The number of seedlings in the ‘S+ L− P−’ and control treatment (without parent plants) increased with time. There were significant differences among control, ‘S+ L−’ and ‘S+ L− P−’ treatments at all times ($P < 0.05$), with the exception of September between the treatments with and without parents.

**Root box experiment**

The root box experiment showed that there were significant reductions in stem height (40%) and individual biomass (80%) of *E. adenophorum* seedlings when grown with its parents, when compared with those grown without parents (one-way ANOVA; $F_{1,31}^{(height)} = 5.374$, $P < 0.05$; $F_{1,31}^{(biomass)} = 7.126$, $P < 0.05$) (Fig. 6). There were no significant differences in root length among treatments (one-way ANOVA; $F_{1,31} = 0.578$, $P > 0.05$).
Discussion

The reproductive characteristics of invasive plants correlate well with their invasive ability (Barrett, 1983) and invasive plants with high seed production and strong clonal ability have often been reported (Baker, 1965, 1974; Reichard, 1997; Willis et al., 1999). Reproduction in E. adenophorum may be via seeds or clones. However, its ability for prolific seed production and spread has been widely reported (Auld, 1970; Auld & Martin, 1975; Auld, 1981; Xiang, 1991; Helen, 2003), but little attention has been paid to the characteristics of clonal reproduction and the contribution of such reproduction to populations. In this study, we found that the reproductive characteristics of E. adenophorum populations differed between habitat types, with most reproduction in an evergreen broad-leaved forest occurring through seed production. Whereas in a deciduous broad-leaved forest and a roadside, most reproduction was via vegetative spread. Differences in the number of newly emerged E. adenophorum seedlings produced via seeds between the different habitats were initially small (July) but increased after 8 months (the following March) to approximately 6–10 times more in the evergreen broad-leaved forest when compared with the deciduous broad-leaved forest or roadside. Seeds appear to contribute more to E. adenophorum reproduction in the evergreen broad-leaved forest and less to reproduction in the deciduous broad-leaved forest or roadside sites.

In general, seed availability is a major factor limiting reproduction in many plant populations. Our experiment showed that there were no differences between plots where we added seeds and the control treatment in the evergreen broad-leaved forest, deciduous broad-leaved forest or roadside sites. This indicates that seed resources are not a major factor restricting the reproduction of E. adenophorum populations in these habitats.
Many studies have reported that germination of *E. adenophorum* seeds is light-dependent (Auld, 1981; Sun *et al.*, 1992), and that natural openings within communities promote population expansion [Tripathi & Yadav, 1982; Xiang, 1991; Fromont & King, 1992; McKellar, 1999; State of State of Queensland (Department of Natural Resources and Mines), 2004]. In our study, however, most of the seedlings that arose from seeds occurred in the evergreen broad-leaved forest that had a dense canopy cover and low light levels, whereas fewer seedlings occurred in the deciduous broad-leaved forest or roadside with more open canopies. These results indicate that seedling establishment was not limited by light availability. Thus, we propose that the degree of soil litter cover may regulate seedling establishment.

The ‘S+ L−’ experiment demonstrated that greater number of seeds were able to germinate and become established in July when the litter layer was removed, but that litter did not have an impact later in the season from August to the following May. This indicates that litter cover inhibits *E. adenophorum* seed emergence, but seedling survival once it has emerged is independent of litter cover. The pot experiment showed that litter reduces the number of seedlings during the seedling emergence period. That may be because litter reduces light intensity on the surface, therefore hindering germination of *E. adenophorum* seeds, but it does not influence the seedling growth after emergence. The high number of seedlings in sites may partially conceal the effect of litter, but the data also suggested that litter is not the sole reason for seedling numbers to be low in certain habitats.

The ‘S+ L− P−’ experiment clearly demonstrated that the presence of parent plants inhibited reproduction by seed in the population. The root box experiment demonstrated that the presence of parent plants inhibited the growth of seedlings. In particular, the biomass of individual plants was substantially reduced, which would likely reduce the survival rate of *E. adenophorum* seedlings. These results support previous findings that the growth of *E. adenophorum* seedlings was reduced when grown close to mature *E. adenophorum* plants (Yadav & Tripathi, 1983). This may be because parents of *E. adenophorum* compete strongly for resources (such as nutrients and water) or because mature plants are toxic to seedlings. We believe that both mechanisms are important, but this study did not distinguish between their relative effects.

Some investigations have considered that invasive plants might not become problematic in all habitats. In the absence of favourable conditions, small populations of an invasive species may establish, remain present but not spread, because characteristics of the population structure and reproduction may be different from other populations in infested sites (Mack, 1996; Sakai *et al.*, 2001). Other research has indicated that invasive plants generally have an r-strategy but may change between r-strategy and K-strategy in different sites (Kolar & Lodge, 2001).

Because several studies have shown that *E. adenophorum* is dependent on high-light conditions [Auld, 1981; Tripathi & Yadav, 1982; Fromont & King, 1992; Sun *et al.*, 1992; McKellar, 1999; State of Queensland (Department of Natural Resources and Mines), 2004], it can be presumed that differences in the light conditions among different habitats regulate differences in plant growth and influence reproduction patterns. In our study, light resources in the evergreen broad-leaved forest were generally low and patchy. Hence, mature plants were sparse and grew weakly, enabling seedlings to better compete for resources. The r-strategy was invoked and reproduction was predominantly by seeds. In contrast, in the more open deciduous broad-leaved forest and roadside, the light availability was high, and the parent plants grew strongly, were abundant and inhibited any seedling emergence from seeds. Thus, the population reproduced primarily by clones that could grow quickly and compete with the mature plants, utilising a K-strategy. Reproduction via clones may create monospecific stands that fully use the high-resource environment and occupy most of the space, which may present substantial barriers to the establishment and restoration of natural vegetation.

Further research on how habitat conditions influence the ‘rules’ by which *E. adenophorum* populations reproduce could help us to better understand the spread of this species and how to effectively manage this invasive plant.

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**References**


