

effects and increased genetic drift (e.g. Eckert et al. 1996; Amsellem et al. 2000), but they also face changes in the selective regime (e.g. Weber and Schmid 1998; Maron et al. 2004). One example of a selective change may be the relaxation in enemy pressure predicted by the ER hypothesis. It has been suggested that natural selection could favour individuals that reallocate resources from defence to other functions, resulting in better growth and competitive ability of invaders in their new ranges (the evolution of increased competitive ability, or EICA hypothesis: Blossey and Nötzold 1995). To date, good evidence exists for escape of some invaders from natural enemies (Memmott et al. 2000; Wolfe 2002; Torchin and Mitchell 2004 but see Agrawal and Kotanen 2003). Evidence for the EICA hypothesis is more equivocal. There is an evidence for reduced allocation to defence by *Spartina alterniflora* (Daehler and Strong 1997) and by *Lythrum salicaria*, though in the latter case no increase in susceptibility to herbivores results (Willis et al. 1999). In *Sapium sebiferum*, an Asian native tree invasive in the US, invasive populations produce less herbivore defence, are larger and flower more than those from the native range (Siemann and Rogers 2001) and are preferentially consumed by generalist herbivores (Siemann and Rogers 2003). Similarly, North American introduced *Silene latifolia* populations were more susceptible to fungal attack, fruit predation and aphid infestation and had a higher reproductive potential than native European ones (Wolfe et al. 2004). However, other studies have provided evidence suggesting that exotic populations do not contain larger or more competitive individuals than the native ones (Willis et al. 2000; Thébaud and Simberloff 2001; Maron et al. 2004). For example, invasive populations of *Alliaria petiolata* are more damaged than native ones by a specialist herbivore when tested in the native range (Bossdorf et al. 2004b), but are less competitive in the absence of herbivores (Bossdorf et al. 2004a). Thus although the ER and the EICA hypotheses are logical and appealing, no clear picture yet exists regarding their contribution to plant invasions.

To investigate the role of ER and EICA in the invasion of common ragweed, *Ambrosia artemisiifolia* L. (Asteraceae) in France, we combine field surveys in 29 natural populations and transplant experiments in four common gardens in the native and in the introduced range. *A. artemisiifolia* is a North American native weed currently invading the valleys of the Rhône and Saône rivers. This species presents an interesting subject for testing these hypotheses. Indeed, it possesses elaborate systems of chemical (e.g. sesquiterpene lactones: David et al. 1999) and structural defence, which could be modified during the invasion. In addition, no other species of *Ambrosia* is native in the invaded area, making it unlikely that specialist herbivores or pathogens could shift from close relatives to this species. *A. maritima*, the only congener native to Europe, grows in the Mediterranean region.

We addressed the following questions to investigate the role of natural enemies in the invasion of this plant: (1) Are ragweed plants less damaged by herbivores and

parasites in the introduced area as the ER hypothesis predicts? (2) Is there evidence for loss of genetically determined defences against natural enemies in this plant, a basic assumption of the EICA hypothesis? Because many characters are likely to evolve over the course of an invasion, we also compared other life history traits, asking: (3) Are there genetic differences in plant life history characteristics, such as growth, final biomass and age at flowering, between the native and introduced ranges? Our experimental design allowed us to test for genetic differences among populations of origin, ecological differences among sites of the different experimental gardens and non-parallel reaction norms for plastic responses by comparing plants from the same populations of origin across the different experimental common gardens (origin \times continent of experimental site interaction effect).

Material and methods

Study species

A. artemisiifolia (Asteraceae) is a common annual native to North America. This anemophilous species is protandrous and monoecious (Bassett and Crompton 1975). It flowers in summer and starts producing mature seeds in September, which germinate from April to July (Bazzaz 1968). During the eighteenth century, the plant was cultivated in numerous botanical gardens in France (Paris, Lyon and Montpellier). The first French records of this plant in natural habitats include a species list of the Beaujolais region near Lyon from 1863 and a written record of its presence in a *Trifolium pratense* field about 150 km to the northwest of Lyon from 1865 (Anonymous 1876). Subsequently, the plant was sporadically recorded until the Second World War after which it became far more common on species lists and in herbarium collections (Bonnot 1967). More recently *A. artemisiifolia* has spread to the north into Burgundy (Carvin et al. 2003) and south into Provence (BJG, personal observation, Fig. 1). In parallel, and probably independently, this plant also invaded other parts of Europe, from Northern Italy to Russia, and parts of Asia and Australia (Igrc et al. 1995).

Ragweed is an aggressive weed causing yield losses to many crops (Clewley et al. 2001), and is particularly common and abundant in disturbed sites such as abandoned or fallow fields (Bazzaz 1968), road verges (Bassett and Crompton 1975) and construction areas. Besides its economic importance as a weed, this plant represents an important public health concern, for its pollen is highly allergenic (Harf et al. 1992).

Field survey

We compared enemy damage in introduced and native populations of *A. artemisiifolia* in the summer of 2003. We sampled 14 populations in France and 15