

# Can the large ecological amplitude of *Ambrosia artemisiifolia* explain its invasive success in France?

B FUMANAL\*, C GIROD†, G FRIED\*, F BRETAGNOLLE‡ & B CHAUVEL\*

\*INRA, UMR 1210 Biologie et Gestion des Adventices, INRA, Dijon Cedex, France, †16 chemin des châtaigniers, Brignais, France, and

‡Université de Bourgogne, UMR 1210 Biologie et Gestion des Adventices, INRA, Dijon Cedex, France

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## Summary

In order to understand the successful spread of *Ambrosia artemisiifolia* in France, the variability of colonised habitat by this species was studied at 48 locations, from its central to peripheral area of distribution. Each site was characterised by a vegetation survey, a description of the *A. artemisiifolia* population and a soil analysis. Differences in the number of species, Shannon diversity index, evenness index and plant life form spectra were compared among the sites. A total of 276 species occurring along with *A. artemisiifolia* was observed. Therophytes and hemicryptophytes represented more than 80% of all the species. The two most frequent species occurring along with *A. artemisiifolia* were

*Chenopodium album* and *Polygonum aviculare*. Multivariate analysis of vegetation surveys showed that *A. artemisiifolia* has a wide ecological tolerance. It colonises a large range of disturbed habitats differing in terms of vegetation cover, species composition and type of soil. The present study highlights the potential of *A. artemisiifolia* for invading spring crops and all semi-natural or disturbed open areas. The success of its ongoing invasion can be explained by both its generalist character and the existence of vacant ecological niches, which are poorly occupied by the French native flora.

**Keywords:** common ragweed, weed, invasion, generalist species, vegetation survey, disturbed habitat.

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## Introduction

Research into plant invasions has usually focused on the determination of traits that make alien species a successful invader (Roy, 1990). However, other studies have focused on the community point of view and have examined which characteristics of plant communities contribute to their susceptibility to invasions (Mack *et al.*, 2000). Although the mechanisms that make a community more sensitive to invasions still need to be fully clarified, one of the most popular hypotheses establishes a link between species diversity and community resistance to invasions (Elton, 1958). If many studies have shown a negative relationship between community diversity and invasibility (Tilman, 1997), conflicting patterns have also been documented, suggesting the existence of environmental factors co-varying

with diversity (Levine & D'Antonio, 1999). Among these factors, the vulnerability because of vacant or unsaturated niches, the biotic resistance of resident species or the level of habitat disturbance influences the invasibility of the communities (Mack *et al.*, 2000).

Human activities are also suspected to increase the invasibility of communities. Fragmentation of the landscape because of the increase in urbanisation and the coexistence in a complex patchwork of natural, semi-natural and artificial habitats with various degrees of disturbance, may represent favourable conditions for invasive species. Moreover, semi-natural areas and the interfaces between natural and artificial habitats often constitute new habitats that are more susceptible to introduced species (Alston & Richardson, 2006), as few native species are able to occupy them efficiently. Nevertheless, some studies have investigated the

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Correspondence: Bruno Chauvel, INRA, UMR 1210 Biologie et Gestion des Adventices, 17 rue Sully, BP 86510, F-21065 Dijon Cedex, France. Tel: (+33) 3 80 69 30 39; Fax: (+33) 3 80 69 32 62; E-mail: bruno.chauvel@dijon.inra.fr

variability of communities colonised by an invasive species in terms of species number (species richness), relative abundance (equitability), diversity or habitat characteristics (Mack *et al.*, 2000). In the present study, the community and the characteristics of the habitats invaded by *Ambrosia artemisiifolia* L. were analysed.

*Ambrosia artemisiifolia* (common ragweed) is an annual monoecious weed (Asteraceae), characterised by spring germination and late autumnal seed (achene) production (Bassett & Crompton, 1975). *Ambrosia artemisiifolia*, which has no particular seed dispersal mechanism, was introduced into Europe and France in the 19th century, along with seeds of cultivated forage species (Bonnot, 1967). As a consequence, the first *A. artemisiifolia* populations were observed in cultivated areas before spreading widely into ruderal habitats. Few data existed on the spread of *A. artemisiifolia* in France before hay fever-related problems increased at the end of 1960s in the suburb of Lyons, where it was found to be highly colonised (Bonnot, 1967). The species is a source of highly allergenic pollen. In France, *A. artemisiifolia* is now described as one of the most important invasive plant species (Jauzein, 2001; Muller, 2004).

*Ambrosia artemisiifolia*, similar to the majority of invasive plants in France, is mostly favoured by human activities and grows along roads, riverbanks, wastelands and cultivated fields (Bonnot, 1967; Muller, 2004). *Ambrosia artemisiifolia* can often be observed in high densities in sunflower fields, because of the low efficiency of chemical control (Chollet *et al.*, 1999) due to the botanical similarity between the weed and the crop. It seems to be mainly influenced by human disturbances, but even if *A. artemisiifolia* dominates abandoned fields initially, perennial herbs eliminate it in the following years (Bazzaz, 1974). Although the spread of *A. artemisiifolia* in France from the Rhône valley is well documented (Chauvel *et al.*, 2006), the vectors of spread are not clear yet and seem to differ according to habitat type.

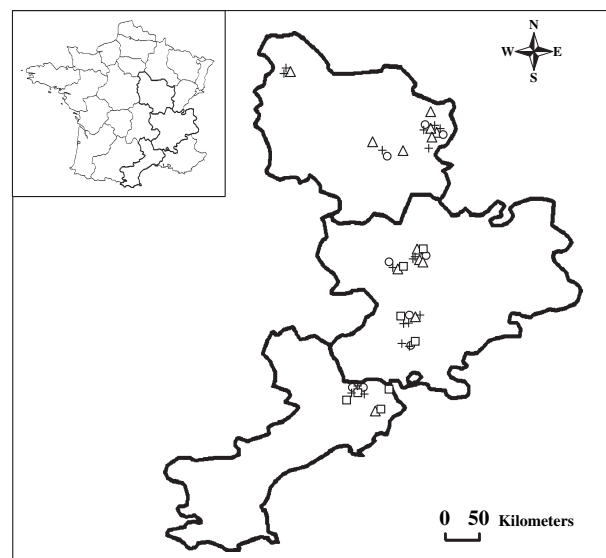
In France (Rhône Valley) and in Switzerland, information on the control of the species is sent to farmers and municipalities to avoid the development of high-density populations (Bohren, 2006). To develop efficient site-monitoring programmes for *A. artemisiifolia*, it is essential to study the behaviour of invasive species related with habitat characteristics, including, the ecological limitations of the species. Thus, it appears necessary to describe the ecology of this species in order to identify the characteristics of invaded habitats. This study sought to determine the characteristics of vegetation and soil composition of all the habitat types where *A. artemisiifolia* develops, in order to assess the variability in environmental factors or management

practices. This study aimed at determining the common characteristics of the habitats occupied by *A. artemisiifolia* and the actual status of this species in the French flora.

## Materials and methods

### Study scope and populations

In order to characterise the range of habitats in France where *A. artemisiifolia* grows, 48 sites containing the plant were studied. The sites studied were sampled into four different habitat types: field crops ( $N_h = 18$ ), roadsides ( $N_h = 9$ ), wastelands ( $N_h = 13$ ) and riverbanks ( $N_h = 8$ ), and were located in the principal and oldest area of spread in France (Muller, 2004), from its central zone in the Rhone Alps region ( $N_1 = 21$ ) to its northern periphery in Burgundy ( $N_1 = 17$ ), and to its southern periphery in the Languedoc Roussillon region ( $N_1 = 10$ ) (Fig. 1 and Appendix S1 for details). The total annual rainfall and the mean winter and summer daily temperatures from 1971 to 2000 (METEO France, <http://www.meteofrance.com/FR/climat/france.jsp> – last accessed November 2007) were 745 mm, 2.5 and 18.3°C for northern sites, 839 mm, 5 and 25°C for central sites, and 773 mm, 8.5 and 23°C for southern sites respectively. All the sampled sites were disturbed to some degree by human activities or by natural phenomena. Field crops were disturbed every year by soil tillage and roadsides by mowing. Wastelands were casually



**Fig. 1** Location of the 48 French sites with *Ambrosia artemisiifolia* populations, studied in 2006. *Ambrosia artemisiifolia* populations were selected in four habitat types across its present central and peripheral invasive distribution area: (□) riverbanks, (○) roadsides, (+) field crops, (△) wastelands. See Appendix S1.

disturbed and the vegetation was at different stages of secondary succession. Finally, riverbanks were naturally but strongly disturbed by annual flooding. No populations were observed in other types of sites, such as forests or meadows.

#### Vegetation surveys

Vegetation surveys were carried out on 300 m<sup>2</sup> plots in the summer of 2006, when vegetative cover and species richness were at their peak. For each plant species, including *A. artemisiifolia*, both presence and coverage were recorded. The total vegetation coverage was evaluated by two different people and coded using the Braun-Blanquet scale, which was transformed into percentage cover (Westhoff & van der Maarel, 1978) that served as input data for further analysis, including six classes from 0.5% for rare plants to 90% for more common plants. Finally, the number of *A. artemisiifolia* plants per square metre in each survey area and the ranges of population sizes in the whole site were also assessed.

#### Soil sampling and analysis

About 1 L of soil from the upper 10 cm was collected in each site after removing the surface litter. Samples were air-dried and sieved with a 2 mm pore-size sieve. Soil analyses were carried out using the French standardised methods edited by the AFNOR group (<http://www.afnor.org/portail.asp> – last accessed November 2007). Samples were analysed for pH KCl (1 mol l<sup>-1</sup>) using the NF ISO 10390 normalised method, for total and active calcium carbonate (CaCO<sub>3</sub>) using the NF ISO 10693 and AFNOR NF X 31-106 Drouineau-Galet normalised method, and for total carbon (C) and nitrogen (N) using the NF ISO 10694 and NF ISO 13878 normalised method. The ratio of total C to total N (C/N) was also calculated as an estimate of soil quality for plant growth. Furthermore, the structural property of soil (texture) was analysed by studying the proportion of particle sizes: clay (<2 µm), silt (2–50 µm) and sand (50–2000 µm).

#### Statistical analysis

Species richness (*S*, species number per site), Shannon diversity index (*H'*) and evenness index (*J*) were used to characterise the plant community and were calculated taking into account all data relative to *A. artemisiifolia*. The frequency *Fr* (presence among all the sites sampled) was also calculated to characterise species fidelity to *A. artemisiifolia*. Shannon diversity index (*H'*) was calculated using species cover as basic values (Hejda &

Pyšek, 2006) and evenness index was calculated as  $J = H' / \ln(S)$ .

The total percentage of therophytes (annuals), hemicryptophytes (overwintering organs at ground level), geophytes (overwintering organs in the soil), chamaephytes (overwintering organs above the soil, 10–30 cm, shrubs) and phanerophytes (high woody plants) was based on the number of counts and evaluated as such. In order to characterise the significant flora associated with *A. artemisiifolia*, Raunkiaer's life form, the preferential germination period, the plant Grime's strategy (Grime, 1974), the status of invasive plant in France, the seed-dispersal system and the photosynthetic pathway (C3/C4) were determined for the most frequent plant species associated with *A. artemisiifolia* (*Fr* > 20%), using bibliographical databases. The status of invasive plants in France was determined according to the latest published invasive plant list (Muller, 2004).

Mean *S*, *H'*, *J*, total vegetation coverage, specific *A. artemisiifolia* coverage and population size were compared among habitat types using one-way ANOVA or Kruskal–Wallis ANOVA when normality and homogeneity of data were not satisfied. Additional pairwise multiple comparison tests of Bonferroni were performed after ANOVA.

In order to evaluate the pattern of site structure relating to vegetation composition, a matrix of the species sampled among all sites was analysed using multivariate correspondence analysis (CA) on presence–absence data (Legendre & Legendre, 1998). Statistics of CA, such as eigenvalues and the percentage of explained proportion of variance for the first three axes, were also calculated.

Soil characteristics were analysed by looking for minimum, lower quartile, median, upper quartile and maximum range of data, in order to evaluate the amount of variation within each soil variable. The relationship between vegetation communities and environmental variables was evaluated using a canonical correspondence analysis (CCA) (Ter Braak, 1986). The CCA created an ordination which maximised the correlation between vegetation and explanatory (biotic or abiotic) variables. Data of species coverage (%) – and the data of the species present in at least two sites (*Fr* > 2%, *n* = 155) – were used for the CCA analysis. A Monte Carlo permutation test (1000 permutations) was used to test the null hypothesis that the variations in vegetation community composition were not related to variations induced by the biotic and abiotic factors. Following Tamado and Milberg (2000), a CCA using the percentage cover of *A. artemisiifolia* was performed as the only explanatory variable to ordinate the distribution of other species along the *A. artemisiifolia* cover gradient.

Statistical analyses were performed using SYSTAT 11 and were assessed at  $\alpha = 0.05$  level.

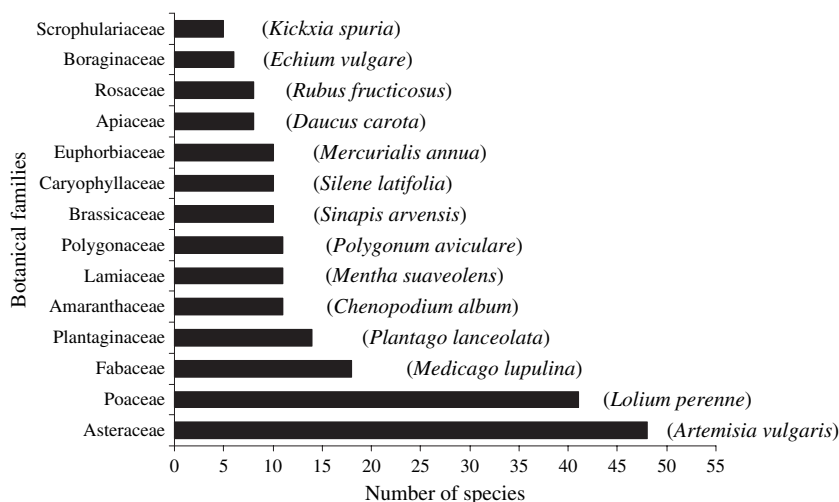
## Results

### Vegetation

A total of 276 plant species belonging to 177 different genera and 51 families were found over the 48 sites studied. The four most represented families were Asteraceae, Poaceae, Fabaceae and Plantaginaceae, including 48, 41, 18 and 14 species respectively (Fig. 2). Among the species sampled, hemicryptophytes (45.8%) and therophytes (40.1%) were the most represented. As expected, geophytes (8.3%), phanerophytes (4.0%) and chamaephytes (1.8%) were less represented, because of the open nature of habitats where surveys were carried out. The wasteland habitats contained more geophytes than roadsides and riverbanks, whereas riverbanks contained more phanerophytes and chamaephytes than wastelands and roadsides. Wastelands, roadsides and riverbanks showed about the same percentages of therophytes (36.5%, 36.5% and 36.3% respectively) and hemicryptophytes (50.6%, 54.8% and 49.6% respectively). The field-crop habitats have a different life form distribution, with a majority of therophytes (58.6%) and a minority of hemicryptophytes (35.4%) and geophytes (6.1%). Obviously, no phanerophytes and chamaephytes were observed in field-crop habitat surveys. The non-native plant species introduced into France occurring along with *A. artemisiifolia* represented 22% (60 species) of the whole vegetation, but only five actual major invasive species were detected: *Buddleja davidii* Franch., *Conyza canadensis* (L.) Cronq., *Conyza sumatrensis* (Retz.) Walker, *Reynoutria japonica* Houtt. and *Senecio inaequidens* DC.

In more than 20% of the sites, a total of 29 plant species were associated with *A. artemisiifolia* (Table 1), while 126 species had a frequency of 4–20% and 121 species were found only once (Fr = 2%). Among the 29 associated species, the most frequent were *Chenopodium album* L. (Fr = 52%), *Polygonum aviculare* L. (Fr = 46%), *Lolium perenne* L. (Fr = 44%), *Plantago lanceolata* L. (Fr = 40%) and *Convolvulus arvensis* L. (Fr = 40%). The two most frequent species (*C. album*, *P. aviculare*) were therophytes and ruderal weeds like *A. artemisiifolia*, and cosmopolitan plants. The three others (*L. perenne*, *P. lanceolata*, *C. arvensis*) were hemicryptophytes and competitive ruderal plants. Among the most frequent plants (Table 1), only one non-native plant, *C. sumatrensis*, is presently considered as an invasive alien in France. Among the most frequent plants (Fr > 20%), all shared a ruderal strategy, some associated with competitive and/or stress-tolerance abilities. The seven plants most frequently associated with *A. artemisiifolia* did not possess a particular seed-dispersal system (barochory). The other plants were anemochores, zoochores or barochores. Among all the species found along with *A. artemisiifolia* across the 48 sites, 36.8% were zoochores, 36.4% barochores, 23.4% anemochores and only 3.3% were hydrochores. A majority of the most frequent plants associated with *A. artemisiifolia* (90%) have a C3 photosynthetic pathway (Table 1), as is the case for the whole plant database (data not shown).

Specific richness (*S*) among sites ranged from six to 47 species (Table 2) and was significantly different among habitats (one-way ANOVA,  $F = 9.891$ ,  $P < 0.001$ ). The number of species found in field crops was lower than in wasteland and riverbank habitats (Fig. 3A). Shannon diversity index (*H'*) showed the same significant pattern of distribution as specific richness (one-way ANOVA,  $F = 7.938$ ,  $P < 0.001$ ),



**Fig. 2** The most 14 represented botanical families (including at least five species) among the 51 observed, belonging to *Ambrosia artemisiifolia* populations under natural conditions. The name of the main frequent species by family is added under brackets at the right part of the bars.

**Table 1** The first 29 plant species associated with *Ambrosia artemisiifolia* (frequency across site, Fr ≥ 20%) with their family, frequency across sites (Fr), Raunkiaer's life form, start of development seasons, Grime's strategy, seed dispersal system and photosynthetic pathway

| Species                        | Family           | Frequency (Fr) | Life form | Start of development | Grime strategy | Seed dispersal | Photosynthetic pathway |
|--------------------------------|------------------|----------------|-----------|----------------------|----------------|----------------|------------------------|
| <i>Ambrosia artemisiifolia</i> | Asteraceae       | 100            | T         | Spring summer        | R              | Barochore      | C3                     |
| <i>Chenopodium album</i>       | Amaranthaceae    | 52             | T         | Spring summer        | R-CR           | Barochore      | C3                     |
| <i>Polygonum aviculare</i>     | Polygonaceae     | 46             | T         | Spring summer        | R              | Barochore      | C3                     |
| <i>Lolium perenne</i>          | Poaceae          | 44             | H         | Autumn               | CR             | Barochore      | C3                     |
| <i>Plantago lanceolata</i>     | Plantaginaceae   | 40             | H         | Ind                  | CR             | Barochore      | C3                     |
| <i>Convolvulus arvensis</i>    | Convolvulaceae   | 40             | H         | Spring summer        | CR             | Barochore      | C3                     |
| <i>Artemisia vulgaris</i>      | Asteraceae       | 38             | H         | Spring               | CR             | Barochore      | C3                     |
| <i>Polygonum persicaria</i>    | Polygonaceae     | 38             | T         | Spring summer        | R              | Barochore      | C3                     |
| <i>Papaver rhoeas</i>          | Papaveraceae     | 35             | T         | Autumn spring        | SR             | Anemochore     | C3                     |
| <i>Cirsium arvense</i>         | Asteraceae       | 33             | G         | Winter spring        | SR             | Anemochore     | C3                     |
| <i>Setaria viridis</i>         | Poaceae          | 33             | T         | Summer               | nd             | Zoochore       | C4                     |
| <i>Fallopia convolvulus</i>    | Polygonaceae     | 29             | T         | Winter spring        | R              | Anemochore     | C3                     |
| <i>Rumex crispus</i>           | Polygonaceae     | 27             | H         | Ind                  | CR             | Anemochore     | C3                     |
| <i>Mercurialis annua</i>       | Euphorbiaceae    | 27             | T         | Spring               | nd             | Zoochore       | C3                     |
| <i>Lactuca serriola</i>        | Asteraceae       | 25             | T         | Autumn spring        | (S)R           | Anemochore     | C3                     |
| <i>Echinochloa crus-galli</i>  | Poaceae          | 25             | T         | Summer               | nd             | Zoochore       | C4                     |
| <i>Elytrigia repens</i>        | Poaceae          | 23             | G         | Winter spring        | CR             | Zoochore       | C3                     |
| <i>Kickxia spuria</i>          | Scrophulariaceae | 23             | T         | Spring summer        | nd             | Zoochore       | C3                     |
| <i>Silene latifolia</i>        | Caryophyllaceae  | 23             | H         | Spring               | nd             | Anemochore     | C3                     |
| <i>Anagallis arvensis</i>      | Primulaceae      | 23             | T         | Spring               | R-SR           | Barochore      | C3                     |
| <i>Daucus carota</i>           | Apiaceae         | 23             | H         | Autumn spring        | nd             | Zoochore       | C3                     |
| <i>Conyza sumatrensis</i>      | Asteraceae       | 23             | H         | Autumn spring        | R              | Anemochore     | C3                     |
| <i>Crepis foetida</i>          | Asteraceae       | 23             | T         | Autumn               | (S)R           | Anemochore     | C3                     |
| <i>Medicago lupulina</i>       | Fabaceae         | 21             | H         | Autumn               | SR             | Barochore      | C3                     |
| <i>Trifolium pratense</i>      | Fabaceae         | 21             | H         | Autumn               | nd             | Zoochore       | C3                     |
| <i>Picris hieracioides</i>     | Asteraceae       | 21             | H         | Spring               | nd             | Anemochore     | C3                     |
| <i>Taraxacum officinale</i>    | Asteraceae       | 21             | H         | Ind                  | R-CSR          | Anemochore     | C3                     |
| <i>Plantago major</i>          | Plantaginaceae   | 21             | H         | Spring summer        | CR             | Barochore      | C3                     |
| <i>Solanum nigrum</i>          | Solanaceae       | 21             | T         | Summer               | R              | Zoochore       | C3                     |
| <i>Cynodon dactylon</i>        | Poaceae          | 21             | G         | Spring summer        | CR-CS          | Barochore      | C4                     |

Raunkiaer's life form: T, therophyte; H, hemicryptophyte; G, geophyte; Grime strategy: R, ruderal; CR, competitive ruderal; SR, stress-tolerant ruderal; CSR, competitive stress-tolerant ruderal; nd, not determined.

whereas evenness index (*J*) was not significantly different (Kruskal–Wallis test,  $H = 1.678$ ,  $P = 0.795$ ) between habitats (Fig. 3B).

The estimated number of individuals in an *A. artemisiifolia* population was smaller and patchy in roadside habitats ( $1375 \pm 595$  plants) than in other sites (field crops  $4657 \pm 843$ ; wastelands  $5639 \pm 1200$ ; riverbanks  $4214 \pm 1417$ ), but no significant difference was detected (Kruskal–Wallis test,  $H = 7.194$ ,  $P = 0.126$ ). The total coverage of vegetation was lower in riverbank habitats ( $40 \pm 8\%$ ) than in other habitats (field crops  $71 \pm 5\%$ ; wastelands  $71 \pm 6\%$ ; roadsides  $57 \pm 11\%$ ), but no general significant difference was detected (Kruskal–Wallis test,  $H = 9.110$ ,  $P = 0.058$ ). Nevertheless, *A. artemisiifolia* coverage was significantly different between habitats (Kruskal–Wallis test  $H = 9.603$ ,  $P = 0.048$ ), with higher levels in field crops ( $28 \pm 7\%$ ) than in other habitat types (roadsides  $13 \pm 1\%$ , wastelands  $12 \pm 5\%$ , riverbanks  $12 \pm 3\%$ ).

The CA on presence–absence data summarised the distribution of the 277 species sampled among the 48 sites studied (Fig. 4). The first two CA axes accounted for 9.66% of the variation on the data axes. The first factorial plan encompasses 4.92% and the second, 4.74% of the total variance. The eigenvalues of the first two axes were relatively high (axis 1: 0.53, axis 2: 0.51) and showed the correlation between species and sites. The species were structured according to the habitat types that were previously distinguished during sampling. According to species composition, axis 2 discriminates the habitats based on environmental characteristics, such as soil texture or chemicals. Riverbank and field-crop habitats were well discriminated, whereas wastelands and roadsides were poorly distinguished. The CA indicated the presence of three different ecological habitats based on plant communities, whereas four distinct habitats were initially defined before sampling. Axis 1 of the CA discriminated mostly the southern, central and northern sites according to their latitude.

**Table 2** Vegetation characteristics at the studied sites described by specific richness (*S*), Shannon index of diversity (*H'*), evenness index (*J*) and the total coverage of vegetation

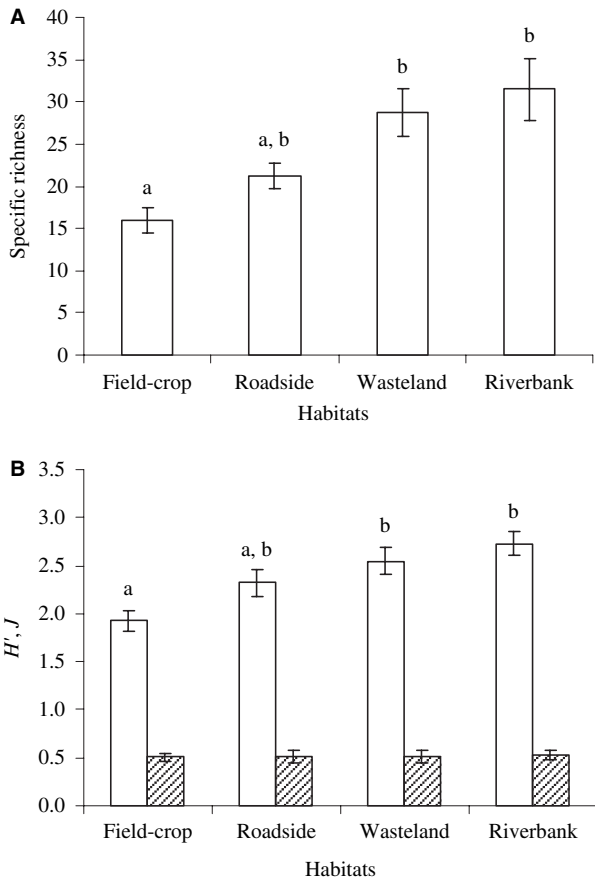
| Site | Specific richness ( <i>S</i> ) | Shannon index ( <i>H'</i> ) | Evenness index ( <i>J</i> ) | Total vegetation cover (%) | <i>A. artemisiifolia</i> cover (%) | <i>A. artemisiifolia</i> density (m <sup>2</sup> ) |
|------|--------------------------------|-----------------------------|-----------------------------|----------------------------|------------------------------------|--|
| 1    | 19                             | 2.827                       | 0.889                       | 90                         | 14                                 | 20   |
| 2    | 19                             | 1.982                       | 0.382                       | 90                         | 57                                 | 500  |
| 3    | 21                             | 2.750                       | 0.745                       | 32                         | 14                                 | 10   |
| 4    | 34                             | 3.318                       | 0.812                       | 90                         | 3                                  | 5  |
| 5    | 24                             | 2.466                       | 0.491                       | 57                         | 14                                 | 15   |
| 6    | 33                             | 2.052                       | 0.236                       | 32                         | 14                                 | 20   |
| 7    | 15                             | 1.732                       | 0.377                       | 57                         | 14                                 | 7  |
| 8    | 10                             | 1.685                       | 0.539                       | 90                         | 32                                 | 100  |
| 9    | 18                             | 2.833                       | 0.945                       | 90                         | 3                                  | 150  |
| 10   | 13                             | 1.626                       | 0.391                       | 32                         | 14                                 | 5  |
| 11   | 40                             | 2.410                       | 0.278                       | 57                         | 0.5                                | 1  |
| 12   | 32                             | 2.608                       | 0.424                       | 32                         | 14                                 | 5  |
| 13   | 47                             | 3.420                       | 0.651                       | 32                         | 3                                  | 1  |
| 14   | 32                             | 1.899                       | 0.209                       | 90                         | 90                                 | 150  |
| 15   | 17                             | 1.920                       | 0.401                       | 90                         | 3                                  | 1  |
| 16   | 20                             | 5.674                       | 14.560                      | 14                         | 3                                  | 1  |
| 17   | 43                             | 2.925                       | 0.433                       | 57                         | 14                                 | 2  |
| 18   | 24                             | 2.275                       | 0.405                       | 90                         | 14                                 | 20   |
| 19   | 20                             | 2.296                       | 0.497                       | 32                         | 14                                 | 10   |
| 20   | 29                             | 2.607                       | 0.468                       | 32                         | 3                                  | 2  |
| 21   | 36                             | 2.730                       | 0.426                       | 90                         | 32                                 | 500  |
| 22   | 14                             | 1.547                       | 0.336                       | 90                         | 14                                 | 3  |
| 23   | 31                             | 2.524                       | 0.402                       | 90                         | 14                                 | 20   |
| 24   | 23                             | 1.036                       | 0.123                       | 90                         | 57                                 | 30   |
| 25   | 15                             | 1.222                       | 0.226                       | 90                         | 0.5                                | 50   |
| 26   | 6                              | 1.257                       | 0.586                       | 57                         | 14                                 | 1  |
| 27   | 21                             | 2.380                       | 0.515                       | 14                         | 14                                 | 5  |
| 28   | 19                             | 2.104                       | 0.431                       | 32                         | 14                                 | 10   |
| 29   | 12                             | 3.285                       | 2.226                       | 57                         | 0.5                                | 1  |
| 30   | 27                             | 2.355                       | 0.390                       | 32                         | 14                                 | 10   |
| 31   | 29                             | 2.069                       | 0.273                       | 90                         | 3                                  | 20   |
| 32   | 9                              | 1.679                       | 0.595                       | 90                         | 14                                 | 10   |
| 33   | 42                             | 3.013                       | 0.485                       | 90                         | 14                                 | 30   |
| 34   | 22                             | 1.915                       | 0.309                       | 32                         | 14                                 | 50   |
| 35   | 28                             | 2.563                       | 0.463                       | 57                         | 14                                 | 140  |
| 36   | 23                             | 3.902                       | 2.153                       | 14                         | 3                                  | 1  |
| 37   | 9                              | 1.081                       | 0.327                       | 90                         | 90                                 | 50   |
| 38   | 15                             | 1.850                       | 0.424                       | 32                         | 14                                 | 1  |
| 39   | 47                             | 3.420                       | 0.650                       | 57                         | 14                                 | 50   |
| 40   | 13                             | 1.155                       | 0.244                       | 57                         | 32                                 | 50   |
| 41   | 13                             | 1.388                       | 0.308                       | 90                         | 14                                 | 30   |
| 42   | 16                             | 1.784                       | 0.372                       | 90                         | 14                                 | 10   |
| 43   | 15                             | 0.950                       | 0.172                       | 90                         | 57                                 | 50   |
| 44   | 19                             | 2.020                       | 0.397                       | 32                         | 3                                  | 3  |
| 45   | 18                             | 3.507                       | 1.853                       | 57                         | 0.5                                | 1  |
| 46   | 21                             | 2.059                       | 0.373                       | 57                         | 14                                 | 30   |
| 47   | 25                             | 2.026                       | 0.303                       | 90                         | 57                                 | 200  |
| 48   | 24                             | 2.404                       | 0.461                       | 90                         | 14                                 | 2  |

Characteristics of *A. artemisiifolia* occurring in each site were represented by their individual coverage and plant density per square metre.

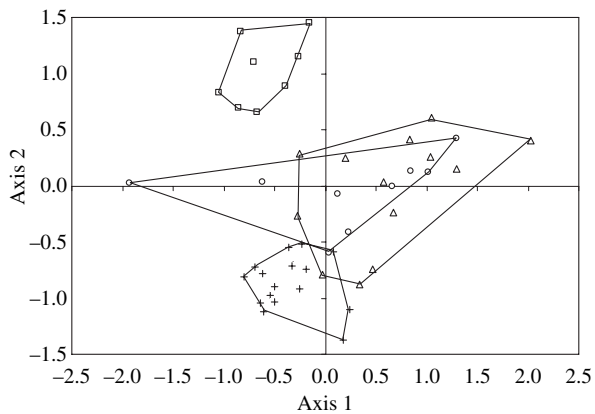
### Soil analysis

The soil texture of the 48 sites studied ranged from sand to clay or silty loam (Appendix S2). The majority of *A. artemisiifolia* populations were observed on sandy soils. The median values among the 48 sites for soil

texture were: 62.4% of sand, 23.8% of silt and 14.7% of clay (Table 3). However, as minimum and maximum values of soil fractional composition revealed, *A. artemisiifolia* was found growing in very different soil textures. The same pattern of variability was found for chemical properties of soils. *Ambrosia artemisiifolia* was



**Fig. 3** Mean ( $\pm$  SE) of the specific richness (A) and of Shannon  $H'$  (open bars)/evenness  $J$  (hatched bars) index (B) across the four habitat types. Same letters indicate no significant differences ( $P > 0.05$ ) using the Bonferroni pairwise test.



**Fig. 4** The factorial correspondence analysis illustrates the population structure based on vegetation composition. The first axes represent 9.66% of the total variance (axis 1: 4.92%, axis 2: 4.74%). The four different habitats of the populations defined *a priori* were represented by different symbols: (□) riverbank, (○) roadside, (+) field-crop, (△) wasteland.

able to grow on acidic or alkaline soils (extreme values of pH KCl: 4.1–8.6), but the majority of sites ranged from 7 to 8 of pH KCl. All the other soil parameters (N,

C/N, organic matter, CaCO<sub>3</sub>) analysed also showed considerable variations between colonised sites (Table 3). Nevertheless, the majority of sites had a median C/N ratio of 10.7, which is very conducive for plant growth.

*Relationship between environmental variations and the distribution of species*

The proportion of variance explained by the first three CCA axes was small (12.9%), because of the large number of species (155), sites (48) and environmental variables (12) analysed. However, the ordination was significant ( $P < 0.001$  – Monte Carlo randomisation test), indicating that the CCA provided a satisfactory summary of the relationship between the species distributions and environmental variables (Table 4, Fig. 5). The distributions of species varied widely in response to the two contrasting soil textures (clay and sand) and, to a lesser extent, to N and pH KCl (Fig. 5). The first CCA axis was most strongly and positively associated with the sand soil texture (Table 4). It was also positively correlated with clay, C/N, pH KCl, organic matter (Om), CaCO<sub>3</sub> and *A. artemisiifolia* coverage (AMBEL-cov), and negatively correlated with (S), N, *A. artemisiifolia* density per square metre (AMBEL-dens), *A. artemisiifolia* population size (AMBEL-pop) and vegetation coverage (VEG-cov) (Table 4). This resulted in sites with higher sand percentage, pH, C/N and S, and lower clay percentage, vegetation coverage, N and organic matter, well separated in ordination space from the sites with opposite characteristics. The second CCA axis was also very strongly and negatively associated with the second clay soil texture, whereas the third axis was negatively associated with soil characteristic variable N (Table 4).

However, the three *A. artemisiifolia* variables (coverage, population size and density) did not have a strong correlation on any axis and were almost opposite to the general trend observed between the other environmental variables and species. Such a pattern shows that *A. artemisiifolia* can develop indifferently in all the sites sampled, without any relationship with the major environmental variables that discriminate the main vegetation.

**Discussion**

While *A. artemisiifolia* was first introduced in fields in 1863 (Chauvel *et al.*, 2006), our study indicates that the species is now present in other areas, such as roadsides, which is very common for non-native species (Christen & Matlack, 2006). The Rhone valley was the main point of naturalisation and expansion of the species, as Allard

| Environmental factor                    | Minimum | 1st Quartile | Median | 3rd Quartile | Maximum | CV (%) |
|---|---------|--------------|--------|--------------|---------|--------|
| Clay % (<2 µm)                          | 1.8     | 7.2          | 14.7   | 25.4         | 42.8    | 65.7   |
| Silt % (2–50 µm)                        | 0.8     | 12.6         | 23.8   | 37.4         | 64.0    | 62.7   |
| Sand % (50–2000 µm)                     | 11.5    | 32.6         | 62.4   | 80.0         | 97.4    | 45.5   |
| N (g/kg)                                | 0.1     | 0.7          | 1.4    | 1.9          | 5.4     | 75.9   |
| C/N                                     | 0.7     | 9.2          | 10.7   | 14.3         | 38.7    | 54.4   |
| pH KCl                                  | 4.1     | 7.2          | 7.7    | 7.9          | 8.6     | 14.8   |
| Organic matter (g kg <sup>-1</sup> )    | 0.6     | 15.1         | 26.8   | 46.6         | 209.0   | 100.1  |
| CaCO <sub>3</sub> (g kg <sup>-1</sup> ) | 0.2     | 9.5          | 94.1   | 309.0        | 761.0   | 119.0  |

For detailed data, see Appendix S2.  
CV, coefficient of variation.

**Table 4** Results of the canonical correspondence analysis (CCA), relating the relative coverage of the 150 plant species occurring at least in two sites to the 12 environmental variables observed in 48 French sites

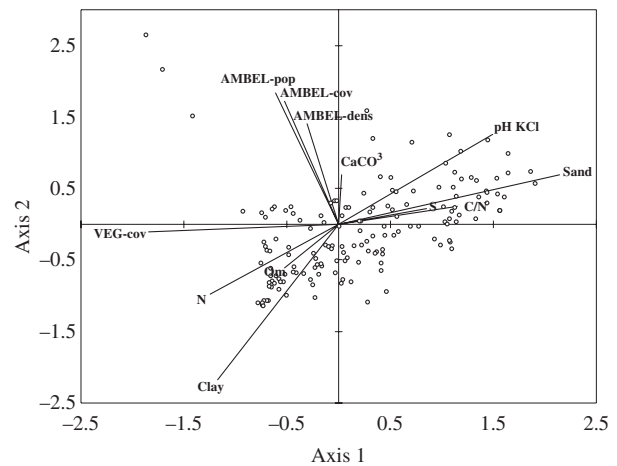
| Variable   | Axis 1 | Axis 2  | Axis 3  |
|--|--------|---------|---------|
| Eigenvalues  | 0.624  | 0.594   | 0.544   |
| Percentage of variance   | 4.564  | 4.342   | 3.977   |
| Cumulative percentage  | 4.564  | 8.907   | 12.883  |
| Cumulative constraint percentage                                 | 13.116 | 25.596  | 37.024  |
| Inter-set correlations of environmental variables                |        |         |         |
| Specific richness ( <i>S</i> )                                   | -0.167 | -0.205  | -0.581  |
| Clay (%)   | 1.034  | -1.246* | 0.198   |
| Sand (%)   | 1.416* | -0.554  | -0.418  |
| N  | -0.801 | 0.124   | -0.719* |
| C/N  | 0.033  | -0.071  | 0.014   |
| pH KCl   | 0.359  | 0.341   | 0.054   |
| Organic matter (Om)  | 0.417  | -0.106  | 0.314   |
| CaCO <sub>3</sub>  | 0.054  | -0.025  | 0.347   |
| <i>A. artemisiifolia</i> density per m <sup>2</sup> (AMBEL-dens) | -0.152 | 0.033   | -0.321  |
| <i>A. artemisiifolia</i> coverage (AMBEL-cov)                    | 0.525  | -0.034  | 0.473   |
| <i>A. artemisiifolia</i> population size (AMBEL-pop)             | -0.222 | 0.224   | -0.209  |
| Total vegetation coverage (VEG-cov)                              | -0.031 | 0.160   | -0.438  |

The species–environment correlations for axes 1–3 were significant ( $P < 0.001$ ) based on a Monte Carlo randomisation test using 1000 permutations.

\*High value per column for the inter-set correlations of environmental variables.

(1943) had predicted many years earlier. Its recent spread is explained by the co-occurrence of different factors, such as the modifications of cropping systems (Chollet *et al.*, 1999) or the increasing urbanisation around cities (Bonnot, 1967). No reliable data indicate whether roadside populations are stable, but the species certainly propagates along road corridors over short distances, but other vectors such as combine harvester or birdseed food (Hanson & Mason, 1985) are also involved in long-distance transport.

**Table 3** Summarised statistics of structural and chemical properties of soil in sites occupied by *Ambrosia artemisiifolia*



**Fig. 5** The canonical correspondence analysis illustrates the relationship between species distribution and environmental variables. The analysis was performed on species coverage data. The environmental variables represented as biplot vectors in the ordination were: *Ambrosia artemisiifolia* population size (AMBEL-pop), *A. artemisiifolia* plant density per square metre (AMBEL-dens), percent coverage of *A. artemisiifolia* (AMBEL-cov), coverage of total vegetation (VEG-cov), specific richness (*S*), carbonate calcium (CaCO<sub>3</sub>), pH KCl, organic matter (Om); nitrogen (N), ratio between carbon and nitrogen (C/N), percentage of soil particle < 2 µm (clay) and percentage of soil particle from 50 to 2000 µm (sand). The proportion of variance explained by the two axes was 25.60% (axis 1: 13.12%, axis 2: 12.48%).

Similar to other introduced species favoured by habitat fragmentation (Lozon & MacIsaac, 1997), *A. artemisiifolia* seemed to be promoted by anthropogenic disturbances and habitat degradation. The pollen is naturally transported by wind over both short and long distances (Clot *et al.*, 2002) and the seeds are dispersed mostly through human activities over both short and long distances. In this context, the occurrence of disturbed sites may be advantageous for the invasive process of *A. artemisiifolia*. The plant demography is characterised by a long-term persisting seedbank (Bassett & Crompton, 1975), but the role of the seedbank is certainly more important in fields and on riverbanks



than on roadsides or in urban areas where the soil is not removed. In the case of *A. artemisiifolia*, the effect of anthropogenic development seems to be the major factor for its invasion (Bazzaz, 1974; Bassett & Crompton, 1975; Chauvel *et al.*, 2006). While specialist species seem to avoid developed areas, generalist species are more tolerant and may even benefit from human development (Richmond *et al.*, 2005).

The large ecological breadth of *A. artemisiifolia*, established on the basis of vegetation and soil characteristics of the habitats colonised, was clearly demonstrated in the present study. Successful and widespread colonising plant species often occur in different habitats, and thus are thought to be characterised by a wide environmental tolerance (Mack *et al.*, 2000). In a changing environment, being able to exploit a wider range of nutrients or habitats may give the invading plants a selective advantage over native species. Even if species-poor communities are assumed to be more prone to invasions than those that are species-rich, *A. artemisiifolia* was found to occur in communities with both low and high species diversity (6–47 species). In the same way, *A. artemisiifolia* did not appear to have any impact on the species diversity of the community as can sometimes be observed with invasive species (Mack *et al.*, 2000; Hejda & Pyšek, 2006). The vegetation sampled over the 48 sites analysed represented distinct ecological groups, and the presence of *A. artemisiifolia* confirmed the generalist (ubiquitous) character of the species. This species can be found in soils with a very wide range of textures and nutrient contents and in very acidic or basic soils, poor or rich in nutrient content.

In the present study, no relationship was found between *A. artemisiifolia* characteristics, such as vigour or plant height, and environmental factors. Thus, *A. artemisiifolia* appeared to be very tolerant to sub-optimal conditions and was able to accommodate various environments. Furthermore, its tolerance to drought stress and adaptation to salinity (Ditommaso, 2004) increase its potential to spread and may explain its presence on very poor substrata. The ability of *A. artemisiifolia* to develop in conditions of drought or nutrient-poor soils can be facilitated by its capacity to create symbiotic interactions with arbuscular mycorrhizal fungi (Fumanal *et al.*, 2006). If its substratum requirements cannot be considered as a constraint to its spread, cold temperature and more precisely the appearance of first frost can limit the development of the species by seed destruction before maturation (Allard, 1943), as is the case for the invasive species *Impatiens glandulifera* Royle (Willis & Hulme, 2002). Even if viable seeds can be produced occasionally, this climatic limitation can explain the low or the non-persistence of *A. artemisiifolia* in Britain (Rich, 1994) or in Lithuania

(Gudzinskas, 1993). From a biological point of view, recent studies showed that the demographic expansion of *A. artemisiifolia* will not be limited by herbivory in its new area of introduction (Genton *et al.*, 2005). Even if *A. artemisiifolia* is present in natural riparian habitats, such as riverbanks south and west of France, no long-lived populations of *A. artemisiifolia* were presently described in forests or in natural meadows. In its native area, *A. artemisiifolia* dominates abandoned fields during the first years, but is then eliminated by the competition of perennial herbs and shrubs (Bazzaz, 1974). If *A. artemisiifolia* appears to be a successful pioneer in early successional habitats with a high degree of disturbance (erosion area, burning places), the species does not seem to be able to compete in later successional ecosystems to develop permanent populations (Bassett & Crompton, 1975). According to Bonnot (1967), *A. artemisiifolia* grows wherever competition is low and in ecosystems regularly disturbed by humans; such a situation explained why *A. artemisiifolia* is not associated with particular phytosociological groups.

In this study, it was observed that *A. artemisiifolia* occurred in different habitats along with some other non-native species and with species from early successional stages. Similar results were observed for other invasive species: Tamado and Milberg (2000) showed that *Parthenium hysterophorus* L. was recorded with a weedy annual flora and with many other non-native species, and Bornkamm (2002) showed that *S. inaequidens* occurred in a large number of vegetation types and in many plant communities. However, *A. artemisiifolia* does not represent a threat to the plant biodiversity of the different invaded areas, as can be clearly observed for other invasive species such as *I. glandulifera* (Hejda & Pyšek, 2006). The two species most frequently associated with *A. artemisiifolia* were *C. album* and *P. aviculare* which are considered as very common and generalist weeds (Jauzein, 2001) in fields as well as in wastelands. The French Flora database SOPHY (<http://sophy.u-3mrs.fr/sophy.htm> – last accessed November 2007) indicated that *C. album* and *P. aviculare* were two species strongly associated with each other in floristic surveys. As *A. artemisiifolia* appeared to be strongly associated with these two species in terms of life history traits and ecology, its spreading potential in France and Europe seems to be very important.

The ability of *A. artemisiifolia* to infest different habitats hinders the establishment of a relevant management framework to control this weed. Even if the control of *A. artemisiifolia* in field crops is sometimes difficult because of agronomical or environmental constraints, a better use of alternative methods and crop rotation should certainly avoid the development of high populations. Furthermore, the development of

*A. artemisiifolia* in different habitat types requires concerted actions (Bohren, 2006) to avoid seed contaminations between these habitats. But the control of the species at the stage of early spread is essential to stop its invasion. Finally, the difficulty of obtaining both control of pollen production (public health) and seed production in different habitats with a unique treatment could also explain the spread of *A. artemisiifolia*.

This study confirmed that *A. artemisiifolia* can invade all open disturbed areas (Bassett & Crompton, 1975; Chauvel *et al.*, 2006). As most American weeds introduced in France, its late emergence favour its development alongside annual spring crops such as soyabean or maize. Another explanation of the success of *A. artemisiifolia* could be that, in France, a few native weeds have a summer cycle (Jauzein, 2001). The success of species such as *Xanthium* spp. or *Amaranthus* spp. could be explained by the existence of empty ecological niches in French flora, where few native species can compete with alien species. In France, *A. artemisiifolia* could be better described as an alien generalist species occupying a free ecological niche or as a winner species (McKinney & Lockwood, 1999) rather than as a 'transformer' species (Richardson *et al.*, 2000).

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## Supplementary material

The following supplementary material is available for this article:

**Appendix S1.** Site locations and habitats in France of *Ambrosia artemisiifolia* populations analysed for vegetation survey and soil analysis. The invasive position of populations and the estimation population size was also signalled.

**Appendix S2.** Detailed data on soil texture with its fractional composition, and chemical properties of soils in sites occupied by *Ambrosia artemisiifolia*. Soil textures were defined according to the USDA soil taxonomy. (nd) not determined.

This material is available as part of the online article from: <http://www.blackwell-synergy.com/doi/abs/10.1111/j.1365-3180.2008.00627.x>

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