Assessing Why Two Introduced Conyza Differ in Their Ability to Invade Mediterranean Old Fields

Christophe Thebaud, Adrien C. Finzi, Laurence Affre, Max Debussche, Josep Escarre


Stable URL:
http://links.jstor.org/sici?sici=0012-9658%28199604%2977%3A3%3C791%3AAWTICD%3E2.0.CO%3B2-0

Your use of the JSTOR archive indicates your acceptance of JSTOR’s Terms and Conditions of Use, available at http://www.jstor.org/about/terms.html. JSTOR’s Terms and Conditions of Use provides, in part, that unless you have obtained prior permission, you may not download an entire issue of a journal or multiple copies of articles, and you may use content in the JSTOR archive only for your personal, non-commercial use.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

Ecology is published by The Ecological Society of America. Please contact the publisher for further permissions regarding the use of this work. Publisher contact information may be obtained at http://www.jstor.org/journals/esa.html.

Ecology
©1996 The Ecological Society of America

JSTOR and the JSTOR logo are trademarks of JSTOR, and are Registered in the U.S. Patent and Trademark Office. For more information on JSTOR contact jstor-info@umich.edu.

©2002 JSTOR
ASSESSING WHY TWO INTRODUCED CONYZA DIFFER IN THEIR ABILITY TO INVADE MEDITERRANEAN OLD FIELDS

CHRISTOPHE THÉBAUD, ADRIEN C. FINZI, LAURENCE AFFRE, MAX DEBUSBESCHE, AND JOSEP ESCARRE
Centre d’Ecologie Fonctionnelle et Evolutive, C.N.R.S., B.P. 5051, F-34033 Montpellier Cedex, France

Abstract. Researchers have suggested that species–community interactions determine invasion success. Therefore, it is likely that small biological differences between species interact with habitat characteristics to produce distinct patterns of distribution and abundance throughout a new range. In this study we test the hypothesis that differences in the distribution and abundance of species sharing an identical set of “ideal weed characteristics” are explicable in terms of species-specific responses to environmental variation within their new range. Using multifactor experiments, we investigated some of the ecological interactions influencing reproductive success in two very closely related species of annuals having invaded the French Mediterranean region for >150 yr and showing marked differences in their local distribution and abundance patterns. We transplanted seedlings of Conyza canadensis (a species restricted to recently disturbed areas) and C. sumatrensis (a species colonizing early- to mid-successional old fields) at equal densities in three contrasting old fields (6 mo, 4 yr, 17-yr abandonment, respectively) during 1991–1992, a growing season with average rainfall. Individual performances (measured as survivorship, reproductive timing, and reproductive output) were evaluated with respect to: (1) competition with plant neighbors (tested with a weeding treatment), (2) resource availability (tested with nutrient and water addition), and (3) herbivory (tested with chemical limitation). Manipulated factors interacted in a rather complex fashion to influence survivorship and reproduction in both species. However, patterns of relative performance were consistent with relative distribution patterns across Mediterranean landscapes: C. sumatrensis performed better than C. canadensis in all fields, including the youngest one (6 mo old). Herbivory only slightly affected transplant performances. In contrast, competition with plant neighbors had substantial effects on either Conyza species and may be the most important determinant of performance in Mediterranean old fields. The experiment showed unambiguously that the two species differ markedly in their competitive ability, with C. sumatrensis performing better than C. canadensis in the presence of neighboring vegetation. In addition, C. sumatrensis displayed a superior ability to take up and/or to use water and nutrient resources when they become available in competitive environments. We argue that potential physiological or anatomical species differences responsible for this differential susceptibility to local resource reduction by neighbors could involve differences in constructional organization, leaf morphology, and reproductive phenologies.

Key words: annual plants; competition; competitive ability; Conyza canadensis; Conyza sumatrensis; distribution; invasion; invertebrate herbivory; life history; Mediterranean old fields; resource availability; survival.

INTRODUCTION

The introduction of exotic plant species into natural terrestrial ecosystems has been a global phenomenon (Elton 1958) that poses critical problems for the conservation and management of many natural ecosystems (Drake et al. 1989). However, despite growing concern over the negative effects of such invasions and our ability to explain why some species become naturalized and prolific in a new range (Lubchenko et al. 1991), we still know surprisingly little about the determinants of the distribution and abundance of invading plant species at both local and regional scales (Mack 1985, Rejmánek 1989, Richardson and Bond 1991). In the past, the invasiveness of nonindigenous species has been often ascribed to their having a particular suite of life history traits or to characteristics of the invaded communities (Elton 1958, Baker and Stebbins 1965, Baker 1974, Bazzaz 1986). Unfortunately, such generalizations, which are based on correlative studies, suffer many exceptions that hinder their predictive ability (Crawley 1987). Recently, it has been proposed that introduced species may succeed or fail to establish de-
pending on complex interactions between a species and its target community, hence the idea that biological invasions are fundamentally context-specific processes (Simberloff 1985, Crawley 1987, D'Antonio 1993). This view implies that small differences among species in their biology may interact with habitat characteristics to produce distinct patterns of distribution and abundance throughout a new range.

Indeed, an apparent paradox in the literature on invading organisms is the number of apparently identical introductions that follow very different trajectories (Simberloff 1985 for a review). Although there are numerous examples of pairs or groups of closely related, congeneric, species introduced into the same regions and that clearly differ in their observed invasiveness (e.g., Acacia, Amaranthus, Avena, Bromus, Hedychium, Impatiens, Solidago) (Baker 1974, Kruger et al. 1986, Macdonald et al. 1991, Weber 1994), few very experimental studies have been conducted to test the hypothesis that differences in the distribution and abundance of species sharing an identical set of “ideal weed characteristics” are explicable in terms of species-specific responses to environmental variation within the new range (Wu and Jain 1979, Weaver 1984, Perrins et al. 1993). Although these studies provide post facto explanations of the community ecology of invasions after they occur, they make clear that we must understand the mechanisms that affect the strength of interactions with target communities in order to predict invasions (Lodge 1993). That is, we must determine how variation in the qualities of potentially similar invaders alters these interactions and discern the relation between species-specific attributes and the various constraints faced by species as the environmental conditions change across multiple and spatially separated communities.

The work reported here is the first study, as far as we know, in which factors were manipulated in the field in order to investigate some of the ecological interactions influencing performance of two closely related introduced annuals, Conyza canadensis (L.) Cronq. (formerly Erigeron canadensis L., see Cronquist 1943), and C. sumatrensis (Retz.) E. Walker (formerly Conyza albida Willd. ex Sprengel or Erigeron naudini [Bonnet] G. Bonnier, see Guédès and Jovet 1975), in Mediterranean old fields, and to explore the mechanisms responsible for these interactions. The genus Conyza provides one of the foremost examples of intercontinental plant invasions from the New World to the Old World; C. canadensis and C. sumatrensis are now among the most abundant plant species found in Europe (Thébaud and Abbott 1995). These species are indistinguishable on the basis of “ideal weed characteristics,” and effectively co-occur over several millions of square kilometres throughout a variety of biogeographic regions within the new range (Jovet and Vilmorin 1975). However, they often show striking differences in their local distribution and abundance (Rivière 1987, Jauzein 1988, Guillerm et al. 1990). In southern France, where both species have been invading for at least 150 yr (Jovet and Vilmorin 1975; C. Thébaud, unpublished data), we found that C. sumatrensis typically establishes and persists in old fields whose age ranges from 0- to 30-yr abandonment, while C. canadensis is restricted to recently disturbed habitats (Thébaud 1993). Moreover, C. sumatrensis achieves higher densities than C. canadensis in habitats where the two species coexist. Both species lack seed dormancy and do not differ in seed dispersal and germination characteristics (see Methods: Study plants). In addition, we found no difference in their establishment success in a preliminary study (Thébaud 1993). Thus, we hypothesize that differences in postestablishment performance in response to ecological factors may explain their distribution patterns.

The experiment was based on simulated colonizations through transplant introductions in three adjacent old fields that differed markedly in cover and composition of the vegetation because of their differences in time since abandonment. Three factors (competition with plant neighbors, resource availability, and herbi-vores) that are known to influence reproductive success in annuals and may greatly differ across environments (Harper 1977, Crawley 1990, Kadmon and Shmida 1990), were manipulated. In this paper, the specific questions we addressed are: (1) Is the response to changes in environmental conditions similar for the two Conyza species? (2) If differences between species exist, how do they arise? (3) Which factors explain the differences in distribution and abundance between species?

METHODS

Study plants

Conyza canadensis and C. sumatrensis have a pre-dominantly winter-annual life history (Thébaud and Abbott 1995). In the Montpellier area, where the study was conducted, most seeds emerge in fall (late August–October) and individuals overwinter as a rosette, bolt in spring (April–June), and begin flowering at the end of July. Seeds that do not germinate in the fall can emerge in the spring. Such individuals may also flower in summer of the same year. However, seedlings from the spring cohort generally experience very high post-emergence mortality through desiccation in the Mediterranean region (C. Thébaud, unpublished data). Hence, the fall cohort is numerically much more important than the spring cohort in our study area. Plant architecture is very similar in both species: one erect main stem with an apical panicle of capitula. They differ in certain subtle morphological characters; for example, C. sumatrensis has heavier stem and leaf pubescence and has flower heads without the minute ligulate ray florets possessed by C. canadensis. Both species are self-fertile (Mulligan and Findlay 1970, Thé-
Capitula are small (C. canadensis: 4.0 mm length × 2.2 mm base width; C. sumatrensis: 4.7 mm length × 2.4 mm base width; Thébaud 1993) and flower sequentially within an individual, hence the flowering period typically spans 1–4 mo. Both species produce seeds with a high dispersal ability (Andersen 1993). Seeds are monomorphic for dispersal characters: they are very light (C. canadensis: 4.74 ± 0.06 μg; C. sumatrensis: 4.50 ± 0.12 μg; n = 5 lots of 50 seeds; two-sample Student’s t test for difference among species, P > 0.1) and all bear a pappus that facilitates wind transport. Seeds are dispersed from mature capitula within 1–2 d, depending on weather conditions. Both species have similar germination requirements for light and temperature (Zinzolker et al. 1985, Chin 1987, Thébaud 1993). There is no dormancy and longevity in laboratory conditions is only 2–3 yr (Hayashi 1979, Chin 1987).

**Study sites**

Three old fields were chosen at the CEFE-CNRS experimental area near Montpellier, southern France (43°39' N, 3°51' E, elevation 60 m above sea level). These sites were created by abandoning mowing and ploughing at various dates: 1974, 1987, and 1990. The “6-mo-old field” (6MF) had been mown twice a year prior to the study, with Dipolotaxis erucoides, Cirsium arvense, Sonchus oleraceus, Papaver dubium, and Bromus madritensis the most common species at the time of the study. The “4-yr-old field” (4YF) was dominated by Dactylis glomerata, Medicago polycarpa, Daucus carota, Plantago lanceolata, and Scabiosa maritima. The “17-yr-old field” (17YF) has undergone secondary succession without further disturbance since abandonment, with Avena spp., Bromus spp., Vicia lutea, Centaurea collina, and Rubus ulmifolius as dominants. This field was bordered by a holm oak (Quercus ilex) copse to the east and may thus experience the confounding effects of successional age and copse boundary. Both C. canadensis and C. sumatrensis were found on all sites before initiation of the experiment (Lavorel 1991). The climate is Mediterranean, with precipitation averaging 592.4 mm (77% of the total) between October and May, and 173.8 mm between June and September for a total of 766.2 mm per year. Monthly rainfall and mean temperatures during the course of the study were not significantly different (t tests for a single observation and the mean of a sample, Sokal and Rohlf 1981; P > 0.10) from the 23-yr averages. Climate data for the study site are given in Fig. 1.

**Environmental measurements**

Three soil samples were collected from each field site on 29 March 1991. Each sample consisted of eight 2.5 cm diameter × 0–10 cm deep cores taken from evenly spaced locations between the experimental plots. Samples were analyzed by INRA, Arras, France, for total organic matter, total N, organic C, NO₃⁻, NH₄⁺, cation exchange capacity (CEC), pH, and available P, K, Ca, and Mg.

Soil moisture content was measured every 2 wk from 30 March to 24 October 1991. Four soil samples were taken from areas immediately adjacent to experimental plots within each field site; each sample was a composite of two 0–10 cm deep cores. Soil moisture was determined gravimetrically after drying the samples at 105°C for 48 h.

![Fig. 1](image-url) Monthly rainfall and temperature data for the study site: (A) mean monthly rainfall (and 1 SE); (B) monthly rainfall for March 1991 through February 1992 plus amounts of water added for the resource treatment (hatched bars) during the experiment; (C) mean monthly temperature.
We measured photosynthetically active radiation (PAR, 0.4–0.7 μm wavelengths) at 5 cm from soil surface and above the canopy in experimental plots where vegetation was left intact using a long sensor (DELTAS, Decagon Devices, Pullman, Washington, USA) with a light-sensitive area of 600 × 10 mm on clear days at midday on 28 March, 21 May, 12 June, and 5 July. Light penetration was determined as the ratio of PAR 5 cm above the soil surface to that above the vegetation. Mean values were computed on a plot basis.

Site manipulation and experimental design

In February 1991, we delimited a uniform area of 50 m² in each of the three fields. These areas were surrounded by wire fencing (4 cm mesh, 0.8 m tall) anchored to the ground to prevent damage by rabbits (Oryctolagus cuniculus). Each experimental area was divided into rows of 10 rectangular plots, 1 × 0.4 m, with a 0.5-m buffer zone between plots to reduce edge effects and to provide access for manipulation and plant censusing.

We used a factorial design in which all possible combinations of three treatments were established. The treatments were: (1) Vegetation removal, hence no aboveground competition from neighboring plants, vs. vegetation left undisturbed ("Competition"); (2) Addition of nutrients and water in combination to the soil vs. no addition ("Resource"); (3) Application of insecticides and molluscicide to reduce the impact of phytophagous invertebrates vs. water-only spray, used as a control for the addition of water with insecticide ("Herbivory").

The combination of these three treatments and their controls resulted in a total of eight treatment combinations. A complete randomized design with five replications of each treatment combination was used on each of the three sites, to give a total of 40 plots per field site or 120 plots in total.

For the vegetation removal treatment, all aboveground vegetation was removed by hand weeding on 3 March 1991, with the soil disturbed as little as possible. A 20 cm wide buffer zone was also cleared of vegetation around the plot to reduce shade or root competition from outside the plot. Resprouting and germinating plants were periodically removed by hand over the course of the experiment.

For the herbivore exclusion treatment, the plot received two kinds of insecticides and a molluscicide in order to maximize protection against invertebrate herbivores. Dursban is an insecticide and nematocide (2% chlorpyrifos by mass; DowElanco, France) used in granular form against soil insects and soil nematodes. In this experiment, it was applied twice, immediately prior to transplanting and 2 mo later, directly on the treated plots at an agricultural rate (3 g/m²). Baythroid is a broad-spectrum contact insecticide (5% cyfluthrin, Bayer, Germany) against both leaf-chewing and sap-feeding insects. In this experiment, it was applied at a concentration of 70 mg/L using a hand-held hydraulic sprayer. Each plot was sprayed on windless days, approximately every 2 wk when the plants were actively growing, and every month towards the end of the season (after 1 July). We sprayed an equal amount of water on those quadrats not receiving any insecticide. Méta, a molluscicide (pellets, 5% metaldehyde, Rhône-Poulenc, France), was applied on the plot and its periphery on three occasions, 19 March, 1 April, 3 May, at a rate of 0.3 g/m². During the study, we observed no signs of phytotoxicity. The possible effect of insecticide applications on the transplant performance was tested in an insect-free greenhouse. Six weeks after transplanting the treatments did not differ in individual rosette size, root and leaf dry biomass, or in leaf area (one-way ANOVA; P > 0.05 for all traits in both species), indicating that possible nutrient inputs through insecticide application were unlikely to be important.

For the resource addition treatment, we applied fertilizer (16–10–12 NPK; Plantacote 8M, Schering, Agrochimie, Germany) in granular form in equal amounts every 2 wk for 10 wk, for a total equivalent to 300 kg/ha nitrogen, 187.5 kg/ha phosphorus, and 225 kg/ha potassium. Approximately 75% of the nitrogen was applied in soluble form as ammonium and nitrate nitrogen. The remaining 25% of the nitrogen was applied in slow release form to allow for nitrogen supply throughout the study. Nutrients were regularly scattered on the soil surface of the plots. Water addition was carried out at regular intervals (X ± 1 SD = 8.6 ± 3.4 d, range: 7–19, n = 18) between 5 April and 6 September. We applied various amounts of water, never exceeding 20 mm/wk (Fig. 1). Plots were watered via a hose with a fine sprinkler attachment to allow the water to soak into the soil and to minimize lateral movement of water. We applied a total of 300 mm over the study period.

Transplantation of the seedlings

In September 1990, seed material was collected in large sympatric populations throughout an old-field site in nearby Montpellier. Seeds were air-dried and stored at room temperature in paper bags until sowing.

Between 11 and 14 December 1990, we sowed seeds in bedding cells filled with a 1:2:2 mixture of sterilized sand, peat, and study site soil. The trays were set on a greenhouse bench under supplemental light to stimulate and synchronize germination. Germination occurred in ∼3 wk. In early February 1991, the seed trays were moved to a cold frame so as to "harden" the seedlings before transplanting.

Each treatment plot was divided into two equal 0.5 × 0.4 m subplots, each randomly assigned to one of the two target species. During 11–15 March 1991, we transplanted 20 seedlings per species subplot in a regular array with a constant 10-cm interplant spacing. Seedlings were planted at a density intended to minimize intraspecific competition. We planted the soil core.
containing the seedling in a hole the size of the core. Holes for transplanting were formed by pressing a round metal bar into the soil. Soil structure and roots were not otherwise disturbed by planting. The seedlings and their immediate vicinity were sprayed with water on the day of transplanting to minimize transplant shock. Of 4800 transplanted rosettes, 13 died in the 1st wk after transplanting and were immediately replaced. In summary, the experiment was designed as a split-plot within each field (Winer et al. 1991: 365–369), with competition, resource, and herbybl as the whole-plot factors and species as the split-plot factor. The randomization of treatments within fields and target species identity within plots precludes any systematic effect of species or treatments on estimates of species or treatment responses.

Data collection

We recorded survival, and timing of bolting (i.e., when the stem exceeded 1 cm) and flowering events for each experimental plant once every month from April to October 1991, and again in December 1991, and February 1992. Death from desiccation was assumed if shriveled plants were found. We observed no other apparent cause of mortality over the course of the experiment. In May, we scored the level of external evidence of damage by different herbivorous invertebrate guilds on each transplant (detailed results to be reported elsewhere) in order to assess the effectiveness of the herbivore exclusion treatment.

During November 1991, when it was evident that the plant had ceased growth, plants having reproduced were measured for the following characters: inflorescence length and width, and main stem diameter (to the nearest 0.1 mm using a digital caliper) at the base of the inflorescence. We were not able to count total seed number per plant as seeds are minute and are released shortly after they mature. Instead, we estimated proportion of capitula having set seeds (hereafter fruit set), assuming that relative fecundity was well expressed by the combination of the measurements of inflorescence size and fruit set. Unfortunately, we had to eliminate several transplants (84 C. canadensis, 80 C. sumatrensis, all in the 17-yr-old field) from analyses because flowering stalks were chewed off in June within a 2-d period by an unknown chewing insect. As a consequence of damage to the apical meristem, attacked plants produced many small branches through growth stimulation of lateral buds, preventing us from further measuring inflorescence characteristics.

Statistical analyses

We made the choice to test the effects of species and treatments with greater power at the expense of statistically evaluating the “among” field effect (except for survival analysis).

Survival data were analyzed using the LIFETEST procedure in SAS (SAS 1990). We used the log rank statistic to test the null hypothesis that the survivorship curves differ between fields, species, and treatments.

The influence of treatments on the proportions of transplants bolting, surviving to reproduction, and setting seeds was evaluated using the log-linear models of the CATMOD procedure in SAS (SAS 1990). We lumped replicate plots to obtain sufficient cell sizes for reliable estimates by the maximum likelihood method (SAS 1990). The contingency tables sometimes had sparse or empty cells. We thus added a small number to all cells (in this case, 0.0001; SAS 1990), and marginally significant probability levels were interpreted with caution.

We analyzed differences in reproductive traits with multivariate ANOVA (MANOVA) using the GLM procedure in SAS (SAS 1990). Univariate ANOVAs were further used to elucidate among-treatment differences for individual variables. Due to low survivorship in 4YF and 17YF, we carried MANOVA on a subset of treatment combinations after examining whether the ANOVA assumptions were met. Differences among treatments were then tested using planned contrasts (Day and Quinn 1989). To avoid the possibility of pseudoreplication (Hurlbert 1984), we computed mean trait values for each species subplot within replicate treatment plots. In addition, analyses were based on cell means excluding plants that died in order to detect trends among survivors. All variables were transformed by log (nonproportional data) or arcsine transformation (for proportions).

Since the protocol of calculation of chi-squares or $F$ ratios was the same for all the analyses, a full log-linear model or ANOVA table is presented only for the first such analysis as an example. For subsequent analyses only $F$ ratios or chi-squares and $P$ values found to be significant are presented.

RESULTS

Environmental data

Soil characteristics.—In March 1991, the fields did not differ in plant-available macronutrients such as NO$_3$-N, NH$_4$-N, and PO$_4$-P (Table 1). In contrast, organic carbon and matter, total nitrogen, and available potassium varied significantly among the three fields with increasing levels from the youngest (6MF) to the oldest field (17YF). The field sites mostly differed in soil-moisture regimes over the course of the experiment (Fig. 2). Soil surface layer tended to be wetter in the 17-yr-old field than in the other fields during the early growing season. In contrast, soil moisture in summer months was the lowest in the 4-yr-old and 17-yr-old fields. This pattern of water availability showed that water was more limiting in the two oldest fields over the course of the experiment.

Light reduction.—Percentage of full sunlight reaching the rosette level varied significantly with field site along the study period (three-way ANOVA, $P <$
TABLE 1. Soil characteristics in the three field sites. Values are given as means. Identical lowercase letters indicate means that are statistically similar among fields at P < 0.05 using a Tukey test following a one-way ANOVA, n = 3 per field.

<table>
<thead>
<tr>
<th></th>
<th>6-mo-old field</th>
<th>4-yr-old field</th>
<th>17-yr-old field</th>
</tr>
</thead>
<tbody>
<tr>
<td>Organic carbon (g/kg)</td>
<td>10.3c</td>
<td>12.7b</td>
<td>17.4a</td>
</tr>
<tr>
<td>Organic matter (g/kg)</td>
<td>17.7c</td>
<td>21.8b</td>
<td>30.0a</td>
</tr>
<tr>
<td>NO₃ (mg/kg)</td>
<td>6.0a</td>
<td>3.3a</td>
<td>4.3a</td>
</tr>
<tr>
<td>NH₄ (mg/kg)</td>
<td>12.0a</td>
<td>11.7a</td>
<td>10.9a</td>
</tr>
<tr>
<td>N (mg/kg)</td>
<td>1.20b</td>
<td>1.28b</td>
<td>1.83a</td>
</tr>
<tr>
<td>P (g/kg)</td>
<td>0.295a</td>
<td>0.301a</td>
<td>0.339a</td>
</tr>
<tr>
<td>K (g/kg)</td>
<td>0.281c</td>
<td>0.376b</td>
<td>0.482a</td>
</tr>
<tr>
<td>Ca (g/kg)</td>
<td>7.0a</td>
<td>4.0b</td>
<td>6.6a</td>
</tr>
<tr>
<td>Mg (g/kg)</td>
<td>0.098b</td>
<td>0.151a</td>
<td>0.143a</td>
</tr>
<tr>
<td>pH</td>
<td>8.3a</td>
<td>8.1b</td>
<td>8.1b</td>
</tr>
<tr>
<td>CEC (mmol/100 g)</td>
<td>15.2b</td>
<td>17.1a</td>
<td>16.7a</td>
</tr>
</tbody>
</table>

0.001). In March, light penetration was lower in the 4-yr-old (71%) and 17-yr-old (30%) fields than in the 6-mo-old field (84%). Also, light penetration decreased with time in the resource addition treatment relative to controls, reflecting a positive effect of resource addition on aboveground biomass. This difference was larger in the two youngest fields (light penetration in July in control vs. resource: 6MF: 64% vs. 40%; 4YF: 57% vs. 39%; 17YF: 27% vs. 19%), indicating that the plant communities in these fields were more responsive to resource addition in terms of aboveground plant biomass. Herbivore exclusion did not affect light penetration over the March–July period.

Efficiency of herbivory treatment.—The probability of attacks by herbivores, i.e., proportion of plants showing any damage by herbivores on a per plot basis, 3 mo after transplanting, was reduced in plots treated with insecticide and molluscicide (6MF: 42% vs 64%, P < 0.05; 4YF: 34% vs. 60%, P < 0.005; 17YF: 55% vs. 70%, P < 0.05; two-tailed Wilcoxon’s signed rank-sum tests on proportions). The proportion of plants showing moderate-to-high impact of herbivory, i.e., proportion of plants showing >10% of leaf area damaged by herbivores on a per plot basis, 3 mo after transplanting, was also reduced by the herbivore exclusion treatment with no trends among fields (6MF: 2% vs. 11%, P < 0.005; 4YF: 3% vs. 8%, P < 0.005; 17YF: 3% vs. 8%, P < 0.01; two-tailed Wilcoxon’s signed rank-sum tests on proportions).

Transplant survival

In the three fields, high mortality in early autumn was essentially due to postreproductive senescence in both species. This was the only major source of mortality in the 6-mo-old field. By contrast, in the 4-yr and 17-yr-old fields, a first period of high mortality occurred during early summer with 19% and 39%, respectively, of all transplants dying within 5 wk. Therefore, survival varied dramatically and significantly among fields for both species (χ² = 399.7, df = 2, P < 0.001). There were significant differences in survival between species across field sites (χ² = 98.04, df = 1, P < 0.001). Conyza sumatrensis survived significantly better than C. canadensis at all field sites (6MF: χ² = 33.8, df = 1, P < 0.001; 4YF: χ² = 66.7, df = 1, P < 0.001; 17YF: χ² = 147.0, df = 1, P < 0.001).

In the 6-mo-old field, C. sumatrensis had survived somewhat better than C. canadensis, but the magnitude of the difference in life-span was not large (42.0 ± 2 wk and 39.3 ± 0.2 wk [mean ± 1 se], respectively). The difference in survival between species was mostly influenced by resource availability (χ² = 38.5, df = 1, P < 0.001). Survivorship of C. sumatrensis increased with resource availability, while resource addition had no significant effect on C. canadensis (Fig. 3A, D). The probability of survival to reproduction for C. sumatrensis (99%) was higher than that for C. canadensis (93%). Analysis of the frequency data showed that this difference between species was significant (Table 2). For both species, survival to reproduction was reduced by competition, but there was no significant difference between species responses (Fig. 4). Herbivory weakly,

![Fig. 2. Moisture availability over the study period in the 6-mo-old field (●), 4-yr-old field (□), and 17-yr-old field (○). Stars indicate that there are significant differences among fields (one-way ANOVA; P < 0.05).](image-url)
but significantly, reduced survival to flowering, but we detected no differences in how it affected species.

In 4-yr- and 17-yr-old fields, survival of both species was strongly affected by competition and resource availability (Fig. 3B, C, E, F). However, *C. sumatrensis* had survived better than *C. canadensis* under competitive conditions (4YF: $\chi^2 = 75.1$, df = 1, $P < 0.001$; 17YF: $\chi^2 = 89.4$, df = 1, $P < 0.001$). Also, resource addition greatly enhanced survival of *C. sumatrensis* in the competition plots, in contrast to the other species (4YF: $\chi^2 = 60.7$, df = 1, $P < 0.001$; 17YF: $\chi^2 = 468.7$, df = 1, $P < 0.001$). These differences in how species responded to competition and resource availability resulted in *C. sumatrensis* surviving much longer than *C. canadensis* (4YF: $36.5 \pm 0.3$ wk vs. $32.1 \pm 0.3$ wk; 17YF: $33.2 \pm 0.4$ wk vs. $25.4 \pm 0.5$ wk). The prob-
Table 2. Analysis of frequencies of survival to flowering among species and treatments. Best fitting log-linear models. Parameters estimated using maximum likelihood method. Replicate plots were lumped to maintain sufficient sample sizes for the maximum likelihood analysis. A nonsignificant likelihood ratio indicates that the model is a good fit for the data. All degrees of freedom except for likelihood ratio are one.

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>6-mo-old field</th>
<th>4-yd-old field</th>
<th>17-yd-old field</th>
</tr>
</thead>
<tbody>
<tr>
<td>Species</td>
<td>25.56***</td>
<td>44.25***</td>
<td>20.28***</td>
</tr>
<tr>
<td>Competition</td>
<td>16.95***</td>
<td>25.59***</td>
<td>11.50***</td>
</tr>
<tr>
<td>Resource</td>
<td>23.90***</td>
<td>3.10</td>
<td>71.38***</td>
</tr>
<tr>
<td>Herbivory</td>
<td>5.99*</td>
<td>0.00</td>
<td>0.12</td>
</tr>
<tr>
<td>Survival</td>
<td>251.86***</td>
<td>167.81***</td>
<td>118.57***</td>
</tr>
<tr>
<td>Spec. × Comp.</td>
<td>...</td>
<td>...</td>
<td>...</td>
</tr>
<tr>
<td>Spec. × Res.</td>
<td>...</td>
<td>...</td>
<td>...</td>
</tr>
<tr>
<td>Spec. × Surv.</td>
<td>28.76***</td>
<td>89.09***</td>
<td>137.66***</td>
</tr>
<tr>
<td>Comp. × Res.</td>
<td>...</td>
<td>22.31***</td>
<td>69.98***</td>
</tr>
<tr>
<td>Comp. × Surv.</td>
<td>19.56***</td>
<td>265.68***</td>
<td>116.50***</td>
</tr>
<tr>
<td>Res. × Surv.</td>
<td>27.14***</td>
<td>158.76***</td>
<td>356.55***</td>
</tr>
<tr>
<td>Herb. × Surv.</td>
<td>7.01***</td>
<td>...</td>
<td>...</td>
</tr>
<tr>
<td>Spec. × Comp. × Res.</td>
<td>...</td>
<td>35.17***</td>
<td>...</td>
</tr>
<tr>
<td>Comp. × Res. × Surv.</td>
<td>...</td>
<td>39.05***</td>
<td>...</td>
</tr>
<tr>
<td>Comp. × Herb. × Surv.</td>
<td>...</td>
<td>3.73†</td>
<td>...</td>
</tr>
</tbody>
</table>

Likelihood ratio    13.47 17.15 42.19***

* P < 0.05, ** P < 0.01, *** P < 0.001.
† This interaction term, though nonsignificant, was included to improve the fit of the model.

The ability of survival to reproduction for *C. sumatrensis* was also significantly higher than that for *C. canadensis* at the two field sites (4YF: 78% vs. 61%; 17YF: 53% vs. 28%; Table 2). For both species, survival to reproduction was reduced by competition and increased by resource availability, but there was no significant difference between species responses (Table 2; Fig. 4). Herbivory effects were not significant for any of the species in any of the two fields.

Reproductive performance

*Bolting time.*—*Coryza sumatrensis* bolted significantly earlier than *C. canadensis* in the three fields (before 15 May vs. after 15 May; 6MF: χ² = 572.2, df = 1, P < 0.001; 4YF: χ² = 207.1, df = 1, P < 0.001; 17YF: χ² = 134.8, df = 1, P < 0.001; Fig. 5, upper graphs). Bolting was accelerated by resource addition (6MF: χ² = 9.7, df = 1, P < 0.002; 4YF: χ² = 22.4, df = 1, P < 0.001; 17YF: χ² = 23.6, df = 1, P < 0.001) and slightly delayed by competition but only in 4-yd-old (χ² = 20.9, df = 1, P < 0.001) and 17-yd-old (χ² = 39.6, df = 1, P < 0.001) fields. However, we detected no differences in how competition and resource availability affected species responses. Species displayed different bolting responses to herbivory only in the 17-yd-old field (χ² = 8.13, df = 1, P < 0.004). Herbivore exclusion treatment accelerated bolting in *C. sumatrensis*, while bolting time was not affected by herbivory in the case of *C. canadensis*. However, in *C. sumatrensis*, the magnitude of the difference between treatments was minimal (<5%).

*Flowering time.*—For both species, competition shifted the temporal distribution of flowering [before 21 September vs. after 21 September] in all three fields (6MF: χ² = 18.9, df = 1, P < 0.001; 4YF: χ² = 27.7, df = 1, P < 0.001; 17YF: χ² = 22.2, df = 1, P < 0.001; Fig. 5, lower graphs). There was no significant difference in how competition affected species in the 6-mo-old field. In contrast, species responded differently to competition in the two other fields (4YF: χ² = 97.4, df = 1, P < 0.001; 17YF: χ² = 23.8, df = 1, P < 0.001). *Coryza sumatrensis* flowered earlier in the presence of competition, while flowering was delayed by competition in the case of *C. canadensis*.

Flowering time was accelerated by resource availability in the 6-mo-old and 4-yd-old field, but the effect was more pronounced in *C. sumatrensis* than in *C. canadensis*.

![Coryza canadensis vs. Coryza sumatrensis](image)

Fig. 4. Proportion of transplants surviving to flowering, setting seeds, and having a fruit set >75%, in relation to the presence (C) and absence (NC) of competition, and the addition (R) and no addition (NR) of supplemental resources for *C. canadensis* and *C. sumatrensis* in (A) 6-mo-old field, (B) 4-yd-old field, and (C) 17-yd-old field.
**Fig. 5.** Proportion of transplants bolting before the 15 May (upper graphs) and flowering before the 21 September among those having flowered (lower graphs) in *C. canadensis* vs. *C. sumatrensis* in relation to the presence (C) and absence (NC) of competition, and the addition (R) and no addition (NR) of supplemental resources, in three field sites: 6MF, 6-mo-old-field; 4YF, 4-yr-old-field; and 17YF, 17-yr-old field.

*canadensis* (6MF: $\chi^2 = 18.0, df = 1, P < 0.001$; 4YF: $\chi^2 = 16.9, df = 1, P < 0.001$; Fig 5, lower graphs).

Herbivory had no detectable effect on flowering time for any of the species.

**Reproductive output.**—The proportion of transplants that set seeds was analyzed using only those plants that had flowered. We found that the probability of setting seeds was directly related to the probability of flowering in both species. However, the proportion of seeding transplants having a fruit set larger than 75% was significantly greater in *C. sumatrensis* than in *C. canadensis* (6MF: $\chi^2 = 38.5, df = 1, P < 0.001$; 4YF: $\chi^2 = 30.0, df = 1, P < 0.001$; 17YF: $\chi^2 = 53.4, df = 1, P < 0.001$; Fig. 4).

Reproductive output differed among species in the three field sites (MANOVA, 6MF: $F = 88.0, df = 4, 29, P < 0.001$; 4YF: $F = 40.9, df = 4, 21, P < 0.001$; 17YF: $F = 17.7, df = 4, 11, P < 0.001$). On average, *C. sumatrensis* produced smaller inflorescences but thicker stems, and displayed higher fruit set than *C. canadensis* (Fig. 6). We found significant differences in how competition and resource availability affected species in the youngest field (6MF) (Table 3). In contrast, there was no significant difference in the responses of *C. canadensis* and *C. sumatrensis* to competition and resource availability in the two other fields (4YF and 17YF). In the 6-mo-old field, *C. sumatrensis* showed an increase in inflorescence length with competition, while inflorescence length for *C. canadensis* displayed no significant between-treatment differences (ANOVA, $F = 15.4, df = 1, 32, P < 0.001$; Fig. 6). Inflorescence size increased more with resource availability in *C. canadensis* than in *C. sumatrensis* (ANOVA, $F = 7.5, df = 1, 32, P < 0.02$ and $F = 5.28, df = 1, 32, P < 0.05$, for inflorescence length and width, respectively). However, *C. sumatrensis* displayed a strong increase in fruit set in response to resource addition, while fruit set showed little change across resource treatments in *C. canadensis* (ANOVA, $F = 16.7, df = 1, 32, P < 0.001$).

Herbivory had no significant effect on reproductive output for any species in any field.

**DISCUSSION**

The field manipulation showed that a variety of ecological factors, namely competition with neighboring plants, availability of soil nutrients and water resource, and herbivore pressure, interact in a particularly complex fashion to influence the relative performance of the two introduced *Conyza* species. The effects of these
Factors vary among habitats, such that population regulation may differ among habitat patches for the two species (see also Mack and Pyke 1983, Reinartz 1984, D’Antonio 1993). More importantly, the results demonstrated that the two introduced Conyza species differed sharply in their survivorship and reproductive performance among old fields. Therefore, changes in habitat conditions may play a large role in determining the pattern of local distribution and abundance of each species. Relative performance of the two species throughout the experiment matched their natural distributions. Compared to C. canadensis the performance of C. sumatrensis was stronger in all habitats, including the most recent old field.

Responses to neighborhood competition and resource availability

Competition with plant neighbors had substantial impacts on either Conyza species, although its relative effect clearly differed among the three old-field habitats. In addition, there is evidence that Conyza sumatrensis had a superior ability to survive in harsher conditions than C. canadensis. Specifically, between-species differences in mortality over the field gradient were such that all C. canadensis transplants died in the competition plots in the two oldest fields, while a fraction of C. sumatrensis transplants were able to grow and to reproduce in the same conditions. Established plant communities in older fields usually result in higher
rates of transpirational water loss in summer (Bazzaz 1979). As a consequence, competition among plants for available water could be more severe in older fields and impede successful establishment of *C. canadensis* while only strongly limiting the abundance of *C. sumatrensis*.

An important difference between *C. canadensis* and *C. sumatrensis* concerns the superior ability of *C. sumatrensis* to take up and/or to use water and nutrient resources when they become available in a competitive environment. Why should *C. sumatrensis* display a greater response than *C. canadensis* to changes in resource availability? Potential physiological or anatomical species differences responsible for differential competitive ability could involve differences in leaf characteristics. *Conyza sumatrensis* produced about twice as many leaves and thus had a total leaf area much larger than even-sized *C. sumatrensis* (C. Thébaud, unpublished data). Although this may favor it through an increase in the photosynthetic surface, it also increases the transpiring surface (Potvin and Werner 1983). Provided that stomatal conductance is similar in both species, it might be that the *C. canadensis* individuals have higher demand for water and are more sensitive to water shortage than *C. sumatrensis* individuals. Additionally, *C. sumatrensis* leaves are covered on both sides with dense but short (0.5 mm) hairs, while leaves of *C. canadensis* are covered with sparse hairs that are longer (1 mm) (Jivet and Vilmorin 1975). This difference in leaf hairiness may further contribute to higher water loss in *C. canadensis* (cf. Niklas 1994). Potvin and Werner (1983) showed that differences in competitive ability between two other closely related composites, *Solidago canadensis* and *S. juncea*, were more linked to morphological traits such as leaf number than to different water use physiologies. This is also likely to be the case in this study. At the prereproductive stage, *C. canadensis* could be more susceptible than *C. sumatrensis* to a shortage in water and/or nutrient resources depending on morphological differences only.

### Effects of herbivores

Several studies have shown how plants introduced into foreign locations can be rapidly colonized by native herbivores (Strong et al. 1984, Auerbach and Simberloff 1988). However, the herbivore assemblages on introduced plants are generally less rich and less specialized than those on the same plants growing in their native range (Strong et al. 1984). Plant species may thus experience less intense herbivory in regions of recent introduction than in their native range (Moran et al. 1986). Thus, introduced plants could be at an advantage when other plants of the communities are themselves heavily attacked (Schierenbeck et al. 1994).

In some cases, however, native herbivores may be an important source of mortality for introduced plants (Kruger et al. 1989). For example, this was observed on *Carpobrotus edulis* and also on *Erodium brachycarpum* and *E. botrys* in California, but, in these particular cases, the native herbivores were mostly small mammals (Rice 1987, D’Antonio 1993). In this study, the herbivory treatment limited the impact of herbivory in an adequate way, though it only slightly minimized the probability of attack by invertebrate herbivores. Nonetheless, the overall importance of herbivory on target species was rather limited owing to the very low frequencies of heavy damage irrespective of treatment. Although herbivory can have important consequences for individual plant fitness (Meyer and Root 1993), it only concerned very small proportions of transplants in this study. As a consequence, invertebrate herbivores had little impact on limiting plant numbers at the population level in both *Conyza* species. Other studies have shown the importance of herbivory for germination or initial seedling establishment stages (Crawley 1989 for a review). However, early seedling mortality in the study populations is mostly related to abiotic stresses, e.g., autumn frosts or spring drought (C. Thébaud, personal observation). The apparent lack of herbivore impacts on the components of reproductive output does not appear to result from inability to take into account seed predation at the flower head level, since seed predation in the study area is mostly exerted by the small bug *Nysius agricola* (Heteroptera: Lygaeidae), which appears to affect very small proportions of the seeds (C. Thébaud, personal observation).

### Phenological variation in bolting and reproductive period

Earlier bolting in the presence of vegetation may be advantageous if it allows plants to reduce the impact
of shading by litter or overtopping vegetation that can both severely limit photosynthetic productivity of plants at the rosette stage (Regher and Bazzaz 1976, Niklás 1988, Facelli and Pickett 1991). In this study, we found that bolting was delayed in response to competition and accelerated by resource addition. This suggests that the cue by which a plant initiates bolting is more related to resource availability than to light in both Conyza species. However, despite this similarity in bolting responses to ecological factors, the two species differed strikingly in bolting time, with C. sumatrensis consistently bolting earlier than C. canadensis. Conyza sumatrensis may thus be at a competitive advantage in vegetated areas, if earlier bolting actually provides a way to reduce the negative impact of shading by neighboring plants. However, the exact way in which differences in time of bolting might contribute to between-species differences in reproductive success remains to be studied. Greenhouse studies have shown a genetic basis for among-species differences and also for among-population (within species) differences in bolting time (C. Thébaud, unpublished manuscript). Furthermore, introduced populations were found to have genetically diverged for this trait to a larger extent in C. canadensis than in C. sumatrensis. Although it is likely that between-species differences in time of bolting reflect evolutionary divergence within the native range prior to the introduction events, the greater population differentiation in C. canadensis indicates that natural selection on bolting time is stronger than in C. sumatrensis. This has yet to be tested. However, it is rather clear that variation in bolting phenology may be a critical issue in determining colonizing success of the species of concern.

The time available for seed production in late flowering species depends strongly on the onset of reproduction if there are unfavorable conditions at the end of the life cycle (e.g., Ritland 1983), i.e., frosts in late autumn/early winter in this study. Differences in the flowering time may thus induce differences in reproductive performance because the longer the reproductive interval the smaller the risk of reproductive failure. Differences in the flowering response of the two Conyza species varied among habitats. In the youngest field (6-mo-old), both species slightly delayed flowering in response to competition. Under harsher conditions in the two other fields, C. canadensis delayed flowering, independently of resource availability, while the onset of flowering was much earlier in the presence of vegetation and even accelerated by resource addition in C. sumatrensis. This acceleration of flowering time in C. sumatrensis may be advantageous in that lengthened reproductive life-spans can allow more time for the development and maturation of fruits when resources are difficult to obtain (e.g., as a result of competition with other plants). The experiment further suggested that an important difference between C. canadensis and C. sumatrensis could concern the higher reproductive effort, i.e., the fraction of resources allocated to the production of flowers plus seed, and potential total number of flowers in C. canadensis. This may result in greater average seed production when the habitats are favorable, i.e., when plants are not subject to resource constraints. However, as we have shown, this may also result in a partial failure of seed production when some competition occurs. By contrast, C. sumatrensis produced smaller, hence lower flower number, and less variable inflorescences. These inflorescences are also supported by stronger stems, which may allow more efficient water flow through wider or more numerous xylem elements (Niklás, 1992). The combination of inflorescence characteristics and reproductive life-span thus permits C. sumatrensis to attain very high fruit set over a wide range of environmental conditions.

Conclusions

This study demonstrates the importance that recondite biological differences between closely related species can have in determining the patterns of distribution and abundance within a new range. It also particularly illustrates how invasion can stem from multiple traits interacting with multiple features of the new range, as Schierenbeck et al. (1994) have recently suggested. Here, differences between C. canadensis and C. sumatrensis in the ability to compete with target communities may in large part account for the dramatic differences in their observed success over the Mediterranean region. These interspecific differences in competitive ability could simply be a reflection of relatively subtle differences in constructional organization, leaf morphology, and reproductive phenologies, but more research is needed to demonstrate that this is really the case. We suggest, as Simberloff (1985) previously did, that reductionist approaches to the study of species–community interactions are useful in understanding the causes for invasions. We further suggest that the use of closely related species, having invaded similar range but followed different ecological trajectories, in the study of invasions is potentially of broad application. Knowledge of how such species are affected by abiotic and biotic factors under a range of field conditions provides a means to identify critical interactions that determine invasion success. This may help in facing the challenge posed by the ever-growing rate at which organisms are still being introduced beyond their natural distributions and ecosystems are directly or indirectly being altered by human activities (Macdonald 1994).

Acknowledgments

We are grateful to Christian Collin for invaluable assistance and companionship during all stages of the fieldwork. For help with data collection we are also grateful to Anne Grossman, Claudie Houssard, Marie Maistre, and in particular to Véronique Alhoune. Michel Grandjanny kindly provided access to weather data. Nabil Kerrouche and François Bretag-
nolle gave helpful statistical advice. We thank John Derek Thompson, Dan Simberloff, Yan Linhart, Mark Rees, Dave Richardson, André Mauchamp, and two anonymous reviewers, who thoughtfully and thoroughly critiqued previous versions of this manuscript. Financial support came from the Ministère de l'Environnement, grant n°922220 (administered by the Fondation Tour du Valat), and institutional funds from the C.N.R.S. The senior author would like to thank J. D. Thompson, D. Simberloff, Y. Linhart, John Lawton, V. Alhouné, F. Bretagnolle, A. Mauchamp, and Jean-Paul Taris for continuous encouragement. Louis Thaler who discussed and challenged the project with him over the years, helping him formulate and clarify his ideas, and the support provided by the Ministère de la Recherche et de la Technologie, the Fondation Tour du Valat, and the ASSEDIC funds. Manuscript preparation was supported by a fellowship from the Human Capital and Mobility Programme of the European Community to CT, and the Natural Environment Research Council (NERC) Centre for Population Biology.

**LITERATURE CITED**


