Invasiveness of alien vascular plants in six arid zones of Europe, Africa and America

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Abstract: Sanz Elorza, M., González Bernardo, F., Serreta Oliván, A. & Gavilán Iglesias, L.P. *Invasiveness of alien vascular plants in six arid zones of Europe, Africa and America. Lazaroa 31: 109-126 (2010).*

Biological invasions are one of the most important components of global change, and have increasing effects on the loss of biodiversity and on human societies as a whole. The difficulties of accurately predicting the fate of a given introduction has led to increased interest in identifying situations where the risk posed by invaders is particularly high. We analyse patterns of plant invasions in arid zones to develop explicit invasion risk protocols. The study zones are five arid regions in three continents: the Mojave and Sonoran Deserts in North America, the Atacama Desert in South America, the Sahara in northern Africa and the Tabernas and Monegros in southwest Europe, (Spain). We test which life-history traits are related to invasiveness in these areas. We use Generalized Linear Mixed Models (GLMM) to model variation between species in invasion success as a function of eight predictors, potentially related to invasiveness: clonality, pollination model, dispersal syndrome, linking to moist soils, seed size, linking to disturbed habitats, salinity tolerance and longevity. We also analyse the differences that exist between the total alien flora in these six areas of the world with respect to the attributes that were considered. From the species perspective, when taxonomic effects were accounted for, only dispersal syndrome and linking to disturbed habitats appeared to be related to the invasive nature of plants. However, if taxonomic effects are not taken into account the variable salinity tolerance is also significantly related. In spite of the fact that the regions have important climatic analogies, there does not appear to be a clear general pattern in the attributes of alien flora, as these are largely dependent on local conditions.

Key words: plant invasions, alien flora, arid zones.

Resumen: Sanz Elorza, M., González Bernardo, F., Serreta Oliván, A. & Gavilán Iglesias, L.P. *Capacidad invasora de las plantas vasculares alóctonas en seis zonas áridas de Europa, África y América. Lazaroa 31: 109-126 (2009).*

Las invasions biológicas constituyen en la actualidad uno de los factores más influyentes del cambio global, con evidente influencia tanto en la pérdida de biodiversidad como en las actividades del ser humano. Ante la dificultad de predecir la ocurrencia de estas invasions, cada vez va cobrando mayor interés la identificación de áreas especialmente susceptibles de ser invadidas. En este trabajo, analizamos los atributos de las plantas alóctonas invasoras de zonas áridas en aras a establecer las bases científicas que permitan identificar y valorar las situaciones de riesgo. Se han elegido para este estudio seis zonas áridas situadas en tres continentes: los desiertos de Mojave y Sonora en América del Norte, el desierto de Atacama en América del Sur, el desierto del Sahara en el norte de África y los subdesiertos de Tabernas y Los Monegros en el suroeste de Europa (España). Hemos estudiado los atributos vitales que parecen estar más relacionados con su capacidad invasora en zonas áridas. Hemos aplicado un análisis GLMM, con la finalidad de inferir el grado de correlación entre el carácter invasor y ocho atributos de las especies: posibilidad de reproducción asexual, tipo de polinización, modo de dispersión de las diásporas, afinidad por substratos húmedos, tamaño de las diásporas, afinidad por hábitats alterados, tolerancia a la salinidad y longevidad. También se analizan las diferencias que existen entre la flora alóctona total de estas seis zonas del Mundo con respecto a los ocho atributos considerados. Cuando se ha eliminado el sesgo que puedan producir

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los parentescos filogenéticos (efecto taxonómico debido a que determinadas familias aportan mayor número de especies invasoras que comparten los mismos atributos), solamente el modo de dispersión de las diásporas y la afinidad por hábitats alterados parecen estar significativamente correlacionados con el carácter invasor. Si no se tiene en cuenta este efecto, también aparece significativamente correlacionada la tolerancia a la salinidad. A pesar de tratarse de regiones con importantes analogías climáticas, no parece existir un patrón común claro en los atributos de sus respectivas floras alóctonas, siendo éstos dependientes en gran medida de las condiciones locales.

Palabras clave: invasiones biológicas, flora alóctona, zonas áridas.

INTRODUCTION

Biological invasions currently constitute one of the most important and striking aspects of global environmental change (THUILLER & *al*., 2007; VILÀ & *al*., 2006; WITTEMBERG & COCK, 2001). The consequences of these invasions are felt in many ways. For example, their effects are seen in the progressive loss of biodiversity, the alteration of biogeochemical cycles, the negative interference with certain human activities and interests, and, in short, in the homogenization of Earth's biota (ATKINSON & CAMERON, 1993). Future global biodiversity scenarios highlight potentially dramatic increases in biological invasions in ecosystems (SALA & *al*., 2000). Once an invasive alien species is established in a territory and the process of invasion has been triggered, the measures needed to control or eradicate it are very expensive and not always effective (PIMENTEL & *al*., 2001). These measures can also cause collateral damage in the environment. For these reasons, preventative action is more useful. Consequently, those studies which are designed to discover the complex mechanisms and patterns which bring about and favour invasion processes can produce predicative models. These models then enable us to identify and evaluate situations where there is a risk.

Two approaches to the study of the phenomenon are (1) the identification of the attributes of the species which enable their success in the process of invasion (invasiveness), and (2) the analysis of the conditions of the habitats that make them more vulnerable to invasion by alien plants (invasibility). Environments and regions with extreme climatic conditions and little human influence seem to be those which have less capacity to receive alien species (SANZ ELORZA

& *al*., 2006; GASSÓ & *al*, 2009). Mountainous areas, the Polar regions, the cold continental steppes and desert and arid areas are examples of these cases. In contrast, those coastal regions which are in mid-latitude countries and which have a high population density are those with the highest numbers of alien flora, both total and invasory (SOBRINO & *al*., 2002). In the case of the arid regions, the study of the phenomenon is especially interesting for various reasons. Although these regions do not have lush vegetation, they do amass a rich flora with numerous endemic species adapted to survive in very concrete and hostile environments. Examples of such areas would be places with scarce and unevenly spread rainfall, areas with high temperatures or wide fluctuations in temperature, or regions with very low relative humidity or drying winds. Other examples would be regions with intense rates of sunshine, severe night radiation frosts, high evapotranspiration values or saline ground. These factors cause species to develop highly specialized adaptations. Such mechanisms could include a reduction in the transpiration surface, a shortening of life cycles, the development of tissues to store water or CAM and C-4 metabolisms. The phenomenon of biological invasions in arid zones has not been widely studied, at least on a global scale, unlike other in habitats and countries where information on the presence and distribution of alien plant species can be found in a variety of published and unpublished accounts and databases (MEYERSON & MOONEY, 2007). However, if the predictions for the future of the climate come true, the extension and distribution of arid zones in the world are going to undergo changes which will require us to take into account the study of all the phenomena and biological processes which are related to them.

The objectives of this study are (1) to determine which life-history traits are related to the invasiveness of alien plants in arid zones; (2) to clarify the differences in the characteristics of the alien flora in several representative arid regions of the world; and (3) to help develop explicit invasion risk protocols for these zones.

MATERIAL AND METHODS

In order to carry out the study, we have chosen six representative arid zones from around the world. These are the Mojave and Sonoran Deserts in North America, the Atacama and Peruvian Deserts in South America, the Sahara in the north of Africa and the regions of Tabernas y Monegros (Spain) in southeast Europe (Figure 1). The Mojave Desert stretches through southwest California. Its climate is characterised by seasonal and daily temperature fluctuations and, on occasions, it suffers from long periods of frost. It includes extremely arid areas, like Death Valley, with average annual mean precipitation of less than 50 mm. The Sonoran Desert extends from the south of California to the south of the Mojave Desert, continuing through southwest Arizona and the northwest of Mexico. Its pattern of temperatures is less cold, although records show an average absolute minimum temperature of - 9.5 ºC (Aguajita/Quitobaquito) and an average absolute maximum of 48.9 ºC (Sierra del Rosario). The annual mean precipitation ranges from 40.22 mm in El Riito to 267.0 mm in Aguajita/Quitobaquito
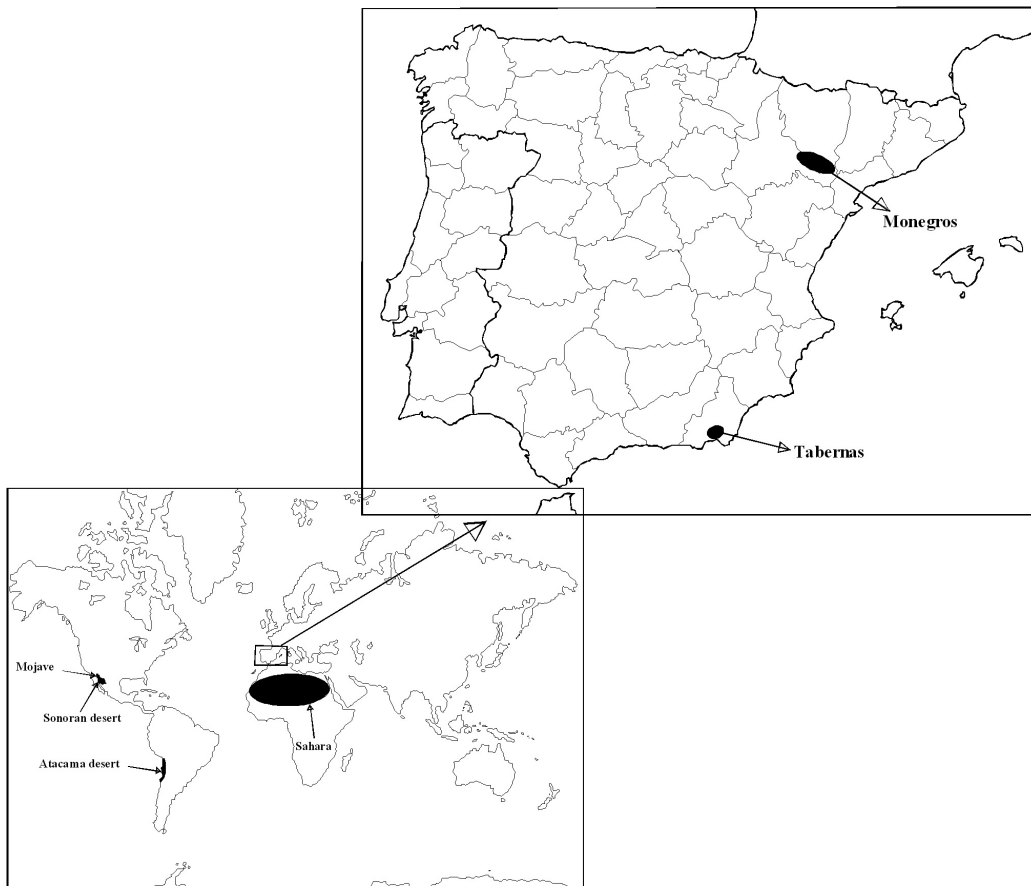

Figura 1.– Geographical location of the six arid areas studied.

(FELGER, 2000). The Atacama and Peruvian Deserts include some of the driest places on earth, with practically no rainfall, (less than 1 mm of average annual rainfall in Arica and Iquique), although at their southern limit (Copiapó) there was 64 mm of annual mean precipitation (MCGINNIES, 1977). The Sahara is the largest desert in the world. It extends from the Atlantic coast of Africa to the Red Sea. It also includes some of the warmest and driest areas in the world. For example, the Great Tanezrouft has an annual mean precipitation of less than 25 mm and in El Azizia, in Libya, the highest temperature in the world was recorded (58 ºC in the shade). The Tabernas Desert extends through southeast Spain and covers an area of approximately 360 km². The annual mean precipitation of most of this area ranges from 180 to 250 mm. The maximum temperatures in the hottest months are above 34 ºC and the minimum temperatures in the coldest months are rather mild with only light frosts. The Monegros Desert is a wide continental steppe area that stretches through the north-eastern part of the Iberian Peninsula in Spain, and covers an area of approximately 2,760 km². Its climate has some extreme temperatures, with maximum summer temperatures that can reach over 40 ºC, and minimum winter temperatures that can be as low as - 12 ºC. The annual mean precipitation ranges from 300 to 420 mm, although it is very irregularly spread out over the year.

For each area, we have catalogued the alien vascular flora from the following sources: Mojave (BALDWIN & al., 2002); Sonoran Desert (FELGER, 2000; NABHAN & al., 2002); Sahara (OZENDA, 1991; QUEZEL & SANTA, 1962-1963; MAIRE, 1952-1980); Atacama and Peruvian Deserts (DILLON, 2005); Tabernas (KUNKEL, 1988; SAGREDO, 1987; DANA & al., 2001); Monegros (MOLERO & BLANCHÉ, 1998; SANZ ELORZA, 2006). We have only taken into account naturalized species, according to the criteria of RICHARDSON & al. (2000), and have not included casuals or sub-spontaneous species. From the information obtained from the cited sources, we considered that a species shows an invasive characteristic when in at least one of the regions studied there are reasons to think that it fulfils the criteria esta-

blished by RICHARDSON & al. (2000) and PYŠEK & al. (2004) relating to the term *invader* when applied to vascular plants. In short, the aforementioned authors define an invasive plant as an alien species with self-sustainable populations without direct human intervention that produces offspring at considerable distances from the parent plants, and thus has the potential to spread over large areas. Invasiveness is quantified as a continuous numeric variable (number of regions where it shows an invasive characteristic).

Once the list of alien naturalized plants in the six arid zones studied had been compiled, a database was created with eight biological and ecological plant traits, according to the scientific literature (PYŠEK & al., 1995; GOODWIN & al., 1999; LLORET & al., 2003; SANZ ELORZA & al., 2006; GASSÓ & al., 2009). These were the traits that could potentially be related to the invasion success of alien species. These variables are clonality (yes, no), pollination model (wind, insects, water), dispersal syndrome (anemochorous, hydrochorous, zoochorous and others that include barochorous, balistochorous, etc.), linking to moist soils (yes, no), seed size (very small if < 1 mm, small between 1-3 mm, medium between 3-5 mm, large between 5-10 mm and very large if > 10 mm), linking to disturbed habitats (yes, no), salinity tolerance (yes, no) and longevity (annual, perennial). We used a test χ^2 in order to determine if significant differences exist between the results obtained in each of the areas.

For statistical analysis, we used Generalized Linear Mixed Models (GLMM) to model the species invasion success (invasiveness) according to the eight predictors previously described. Typical GLM can estimate and test any univariate or multivariate general linear model, including those for multiple regression, analysis of variance or covariance, and other procedures such as discriminant analysis and principal components. The model is:

$$Y = XB + e$$

where **Y** is a vector or matrix of dependent variables (they should be continuous numeric variables), **X** is a vector o matrix of independent variables (they may be either continuous or cate-

gorical dummy variables, according to the type of model), **B** is a vector or matrix of regression coefficients, and e is a vector or matrix of random errors (SEARLE, 1971; WINER, 1971; NETER & *al.*, 1985; COHEN & COHEN, 1983).

After the parameters of the model have been estimated, they can be tested by any general linear hypothesis (in our model, life-history traits are related to the invasiveness of alien plants in arid zones) in the following form:

$$ABC' = D$$

where **A** is a matrix of linear weights on coefficients across the independent variables (the rows of **B**), C is a matrix of linear weights on the coefficients across dependent variables (the columns of **B**). In our model, **C** is an identity matrix. **B** is the matrix of regression coefficients of effects, and **D** is a null hypothesis matrix (null matrix). However, there is a clear bias as far as both the invasive characteristics of the species and their biological and ecological attributes are concerned. This is due to the phylogenetic relationship, and is defined as taxonomic bias. This causes an erroneous increase in the number of degrees of freedom as each species is used as an independent piece of data (BRÄNDLE & *al.*, 2003), with the resulting increase of type-I errors. GLMM enables the phylogenetic effect to be mitigated by means of the incorporation of the taxonomic categories, in our case the genus, as nested random factors. This partly controls the probable lack of independence of the values assumed by the variables in species that are phylogenetically close (GASSÓ & *al.*, 2009).

RESULTS

SPECIES APPROACH

The inventory of the alien flora of the areas studied, extracted from bibliographical sources, lists a total of 347 species although there are notable qualitative and quantitative differences as far as the location of each area is concerned (Table 1).

Accounting for taxonomic relationships, of the eight selected predictors, only two are significantly related to the invasion characteristic (Table 2). These are dispersal syndrome and linking to disturbed sites. If taxonomic bias is not considered, the salinity tolerance (F-ratio = 9.097; p-value = 0.0027) also appears to be significantly related to the invasion characteristic, as halophyte species are concentrated in a few families and genera. With regard to the dispersal syndrome, the wind and rain can be seen to be the main vectors of invasive alien species (Figure 2). As far as linking to disturbed sites is concerned the invasive species are largely ruderal and nitrophilous (Figure 2).

ALIEN FLORAS OF ARID ZONES

The analysis of the differences in the percentages of alien species obtained in each area for each of the predictors, with relation to the overall
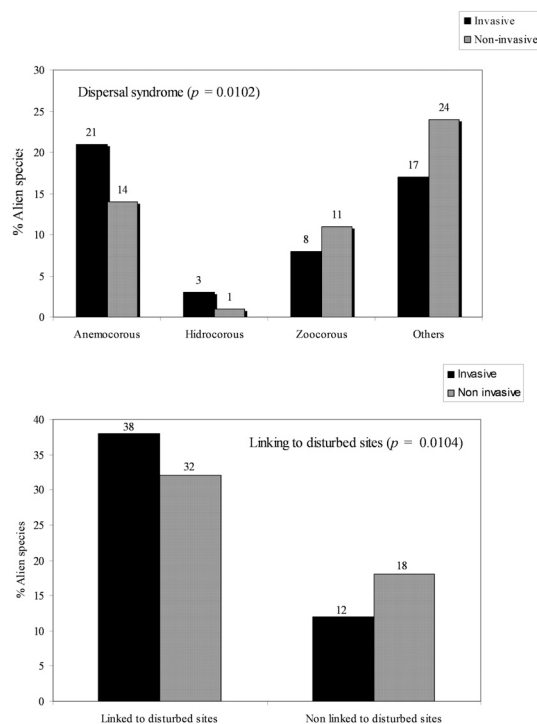

Figura 2. – Characterisation of the alien flora of the arid zones which were studied. Non-significant results have been omitted.

Table 1
Alien flora of the six arid areas studied (+ presence, - absence)

Family	Species	Original geographic range	Mojave	Sonoran Desert	Atacama	Sahara	Tabernas	Monegros
Agavaceae	*Agave americana*	Mexico	-	-	-	-	+	-
Agavaceae	*Agave fourcroydes*	Neotropical	-	-	-	-	+	-
Agavaceae	*Agave sisalana*	Neotropical	-	-	-	-	+	-
Aizoaceae	*Carpobrotus chilensis*	América del Sur	-	+	-	-	+	-
Aizoaceae	*Mesembryanthemum crystallinum*	South Africa	-	+	+	+	+	-
Aizoaceae	*Mesembryanthemum nodiflorum*	Mediterranean-saharian	-	+	-	native	native	+
Alismataceae	*Sagittaria montevidensis*	South America	-	-	-	-	-	+
Amaranthaceae	*Amaranthus albus*	North America	-	+	+	-	-	+
Amaranthaceae	*Amaranthus blitoides*	North America	native	native	-	-	-	+
Amaranthaceae	*Amaranthus blitum*	Tropical s.l.	-	-	-	-	-	+
Amaranthaceae	*Amaranthus deflexus*	South America	-	+	-	-	+	+
Amaranthaceae	*Amaranthus graecizans*	Tropical s.l.	-	+	-	+	+	+
Amaranthaceae	*Amaranthus muricatus*	South America	-	+	-	+	+	+
Amaranthaceae	*Amaranthus retroflexus*	North America	+	+	-	+	-	+
Amaranthaceae	*Amaranthus spinosus*	Neotropical	+	-	-	-	-	-
Amaranthaceae	*Amaranthus viridis*	Tropical s.l.	-	-	+	+	+	+
Anacardiaceae	*Schinus molle*	South America	-	-	native	-	+	-
Anacardiaceae	*Rhus lancea*	África	-	+	-	-	-	-
Apocynaceae	*Catharanthus roseus*	Madagascar	-	+	-	native	native	-
Apocynaceae	*Nerium oleander*	Mediterranean-saharian	-	+	-	-	native	-
Asclepiadaceae	*Cryptostegia grandiflora*	Madagascar	-	+	-	-	-	-
Araceae	*Pistia stratiotes*	Tropical s.l.	-	+	-	-	-	-
Cactaceae	*Cylindropuntia spinosior*	North America	native	native	-	-	-	+
Cactaceae	*Cylindropuntia tunicata*	North America (Chihuahua, Texas)	-	-	+	-	-	-
Cactaceae	*Opuntia ficus-indica*	Neotropical (from Mexico to Colombia)	+	-	-	+	+	-
Cactaceae	*Opuntia lindheimeri* var. *linguiformis*	North America (Texas)	-	+	-	-	-	+
Cactaceae	*Opuntia monacantha*	South America	-	-	-	-	-	+
Capparaceae	*Cleome viscosa*	Sahara, Arabia and Central Africa	-	+	-	native	-	-
Caryophyllaceae	*Agrostemma githago*	Irano-turanian	-	-	-	-	-	+
Caryophyllaceae	*Cerastium glomeratum*	Eurasian	-	+	-	-	native	native
Caryophyllaceae	*Gypsophila paniculata*	Eastern Europe and western Asia	+	-	-	-	-	-
Caryophyllaceae	*Herniaria cinerea*	SE Europe, N Africa and W Asia	-	+	-	-	native	native
Caryophyllaceae	*Sagina apetala*	Holartic	-	-	+	-	-	-
Caryophyllaceae	*Silene conoidea*	Mediterranean-irano-turanian	-	+	-	-	-	native

Family	Species	Origin						
Caryophyllaceae	*Silene nocturna*	Mediterranean	-	-	-	+	native	native
Caryophyllaceae	*Silene rubella*	Mediterranean	-	-	-	+	native	native
Caryophyllaceae	*Silene succulenta*	Central Mediterranean basin	-	-	-	+	-	-
Caryophyllaceae	*Spergularia marina*	Eurasian	+	+	-	-	native	native
Caryophyllaceae	*Stellaria media*	Europe and Mediterranean	+	+	+	-	-	native
Caryophyllaceae	*Vaccaria hispanica*	Irano-turanian	-	-	-	-	-	-
Compositae	*Artemisia biennis*	Eurasian	+	-	-	-	-	+
Compositae	*Artemisia verlotiorum*	China	-	-	-	-	-	-
Compositae	*Aster squamatus*	America s.l.	-	-	-	-	+	+
Compositae	*Bidens bipinnata*	Neotropical	-	-	-	-	-	+
Compositae	*Bidens frondosa*	North America	-	-	-	-	-	+
Compositae	*Carduus nutans*	Eurasian and Mediterranean	+	+	-	-	-	native
Compositae	*Carthamus lanatus*	Mediterranean basin	+	+	-	-	-	native
Compositae	*Carthamus tinctorius*	Paleotropical	-	+	-	-	-	-
Compositae	*Acroptilon repens*	C and W Asia	+	+	-	-	-	-
Compositae	*Centaurea calcitrapa*	Mediterranean basin	+	+	-	-	native	native
Compositae	*Centaurea melitensis*	Mediterranean basin	+	+	+	+	native	native
Compositae	*Centaurea solstitialis*	Mediterranean-irano-turanian	+	+	-	-	-	native
Compositae	*Cichorium intybus*	Eurasian and Mediterranean	+	-	-	-	-	native
Compositae	*Cnicus benedictus*	Mediterranean basin	+	+	-	-	-	native
Compositae	*Conyza bonariensis*	Neotropical	-	+	-	-	+	+
Compositae	*Conyza canadensis*	North America	-	+	-	-	+	+
Compositae	*Conyza sumatrensis*	South America	-	-	-	-	+	+
Compositae	*Cotula australis*	Australia and New Zealand	-	+	-	+	-	-
Compositae	*Cotula coronopifolia*	South Africa	-	+	+	+	-	-
Compositae	*Chrysanthemum coronarium*	Southern Mediterranean basin	-	+	-	+	native	native
Compositae	*Dimorphoteca sinuata*	Southern Africa	-	+	-	-	-	-
Compositae	*Eclipta prostrata*	Neotropical	-	+	-	-	-	+
Compositae	*Euryops subcarnosus*	Southern Africa	-	+	-	-	-	-
Compositae	*Flaveria trinervia*	America s.l.	-	+	-	-	-	-
Compositae	*Galinsoga ciliata*	Central and South America	-	-	native	-	-	+
Compositae	*Gnaphalium luteo-album*	Eurasian	+	+	-	-	+	-
Compositae	*Grindelia squarrosa*	From Wyoming to New Mexico	+	+	-	-	-	-
Compositae	*Hedypnois cretica*	Mediterranean Basin	-	+	-	-	native	native
Compositae	*Helianthus annuus*	North America	-	+	-	-	-	+
Compositae	*Helianthus ciliaris*	Southeastern USA and Mexico	+	+	-	+	-	-
Compositae	*Lactuca serriola*	Europe and Mediterranean	-	+	-	-	-	-
Compositae	*Chamomilla suaveolens*	North America	-	+	-	-	native	native
Compositae	*Pentzia incana*	Southern Africa	-	+	-	-	-	-

Family	Species	Origin						
Compositae	*Pulicaria paludosa*	Europe	-	+	-	-	native	-
Compositae	*Senecio vulgaris*	Cosmopolitan	-	+	+	+	-	native
Compositae	*Sonchus asper*	Europe and Mediterranean	-	+	+	+	-	native
Compositae	*Sonchus oleraceus*	Europe and Mediterranean	-	+	+	+	native	native
Compositae	*Sonchus tenerrimus*	Mediterranean	-	+	-	-	native	native
Compositae	*Silybum marianum*	Europe and Mediterranean	-	+	-	-	native	native
Compositae	*Taraxacum officinale*	Europe and Mediterranean	-	+	-	-	-	native
Compositae	*Tragopogon porrifolius*	Eastern Mediterranean basin	-	+	-	-	-	-
Compositae	*Verbesina encelioides*	North America	-	+	-	-	-	-
Compositae	*Xanthium spinosum*	South America	-	+	-	+	-	+
Compositae	*Xanthium strumarium*	North America	-	+	-	+	-	+
Convolvulaceae	*Convolvulus arvensis*	Mediterranean-irano-turanian	-	+	+	+	native	native
Convolvulaceae	*Ipomoea x leucantha*	Neotropical	-	+	-	-	-	-
Convolvulaceae	*Ipomoea triloba*	Neotropical	-	+	+	+	-	-
Cruciferae	*Brassica campestris*	Eurasian	-	-	-	-	-	-
Cruciferae	*Brassica napus*	Unknown	-	-	-	-	-	+
Cruciferae	*Brassica nigra*	Eurasian	-	+	+	+	-	-
Cruciferae	*Brassica tournefortii*	Mediterranean-irano-turanian	+	+	-	+	-	-
Cruciferae	*Cakile maritima*	Eurasia and Northern Africa	-	+	-	+	-	-
Cruciferae	*Camelina microcarpa*	Eurasian	-	+	-	-	-	native
Cruciferae	*Cardaria draba*	Europe and SW Asia	-	+	-	-	native	native
Cruciferae	*Chorispora tenella*	Eurasian	-	+	-	-	-	-
Cruciferae	*Conringia orientalis*	Irano-turanian	-	+	-	-	-	+
Cruciferae	*Coronopus didymus*	Neotropical	-	+	-	-	-	-
Cruciferae	*Coronopus squamatus*	Eurasia and northern Africa	-	+	-	native	-	native
Cruciferae	*Descurainia sophia*	Europe and Mediterranean	-	+	-	native	native	native
Cruciferae	*Diplotaxis erucoides*	Mediterranean	-	-	-	+	-	native
Cruciferae	*Diplotaxis virgata*	Western Mediterranean basin	-	+	-	-	native	native
Cruciferae	*Draba reptans*	North America	+	-	-	+	-	-
Cruciferae	*Eruca sativa*	Mediterranean-irano-turanian	-	+	-	-	native	native
Cruciferae	*Erysimum cheiri*	Eastern Mediterranean basin	-	-	-	-	-	+
Cruciferae	*Hirschfeldia incana*	Mediterranean-irano-turanian	+	+	-	+	-	native
Cruciferae	*Lepidium campestre*	Europe and W Asia	-	+	-	-	-	-
Cruciferae	*Lepidium perfoliatum*	Eastern Europe and W Asia	-	+	-	-	-	-
Cruciferae	*Malcolmia africana*	S Europe and NW Africa	-	+	-	native	native	native
Cruciferae	*Raphanus raphanistrum*	S Europe, SW Asia and N Africa	-	+	-	-	-	-
Cruciferae	*Sisymbrium altissimum*	Eastern Europe and W Asia	-	+	-	-	-	-
Cruciferae	*Sisymbrium erysimoides*	Southern Mediterranean basin	-	-	-	-	native	-
Cruciferae	*Sisymbrium irio*	Mediterranean-irano-turanian	+	+	+	+	native	native

Family	Taxon	Origin						
Cruciferae	*Sisymbrium orientale*	Mediterranean-irano-turanian	-	-	-	-	native	native
Cucurbitaceae	*Citrullus colocynthis*	Saharian-arabian	-	-	-	native	+	-
Cucurbitaceae	*Citrullus lanatus*	South Africa	-	-	+	-	-	-
Cucurbitaceae	*Cucumis melo*	South Africa	-	-	+	-	-	+
Cucurbitaceae	*Cucumis myriocarpus*	Central and South Africa	-	-	-	-	-	-
Cymodoceaceae	*Halodule wrightii*	Coastal Mexico and Caribbean	-	-	+	-	-	-
Cyperaceae	*Cyperus involucratus*	Madagascar	-	-	+	-	-	-
Cyperaceae	*Cyperus iria*	E Africa, W and C Asia	-	-	+	-	-	-
Cyperaceae	*Cyperus rotundus*	Eurasian	-	-	+	+	native	-
Cyperaceae	*Kyllinga brevifolia*	Neotropical	+	-	+	-	-	-
Chenopodiaceae	*Atriplex rosea*	Europe, C. and SW Asia	-	-	+	-	native	native
Chenopodiaceae	*Atriplex semibaccata*	Australia	+	-	+	-	+	-
Chenopodiaceae	*Atriplex suberecta*	Australia	-	-	+	-	-	-
Chenopodiaceae	*Atriplex wrightii*	North America	-	-	+	-	-	-
Chenopodiaceae	*Bassia hyssopifolia*	Mediterranean-irano-turanian	-	-	+	-	native	native
Chenopodiaceae	*Bassia scoparia*	Mediterranean-irano-turanian	+	+	+	-	-	native
Chenopodiaceae	*Chenopodium album*	Cosmopolitan	+	+	+	-	native	native
Chenopodiaceae	*Chenopodium ambrosioides*	Neotropical	-	-	-	-	+	+
Chenopodiaceae	*Chenopodium berlandieri*	North America	+	+	+	-	-	-
Chenopodiaceae	*Chenopodium foliosum*	Eurasian	native	-	-	-	-	-
Chenopodiaceae	*Chenopodium murale*	Mediterranean s.l.	+	+	+	+	native	native
Chenopodiaceae	*Chenopodium vulvaria*	Mediterranean s.l.	-	-	-	+	-	native
Chenopodiaceae	*Cycloloma atriplicifolium*	Central North America	+	+	-	-	-	-
Chenopodiaceae	*Halogeton sativus*	SW Europe and Northern Africa	+	+	-	native	native	-
Chenopodiaceae	*Salsola tragus*	Eurasia and northern Africa	+	+	+	-	native	native
Chenopodiaceae	*Salsola paulsenii*	Eastern Europe and western Asia	+	+	-	-	-	-
Elaeagnaceae	*Elaeagnus angustifolia*	Temperate Asia	+	+	-	-	-	-
Elatinaceae	*Elatine chilensis*	South America	+	-	+	-	-	-
Euphorbiaceae	*Chamaesyce nutans*	Caribbean	-	-	-	-	+	+
Euphorbiaceae	*Chamaesyce maculata*	Eastern North America	-	-	+	-	-	-
Euphorbiaceae	*Chamaesyce prostrata*	Neotropical	-	-	+	-	-	+
Euphorbiaceae	*Chamaesyce serpens*	Neotropical	-	native	+	-	+	-
Euphorbiaceae	*Euphorbia hyssopifolia*	Neotropical	-	-	+	-	-	-
Euphorbiaceae	*Euphorbia peplus*	Eurasia and northern Africa	-	-	+	native	native	native
Euphorbiaceae	*Ricinus communis*	Eastern Africa	-	-	+	+	+	-
Geraniaceae	*Erodium cicutarium*	Eurasia and northern Africa	+	+	-	native	native	native
Geraniaceae	*Erodium malacoides*	Mediterranean-irano-turanian	-	-	+	-	native	native
Geraniaceae	*Erodium moschatum*	Mediterranean	-	-	+	-	-	-
Gramineae	*Agrostis stolonifera*	Eurasia and northern Africa	+	-	-	native	-	native

Family	Species	Origin	1	2	3	4	5	6
Gramineae	*Apera interrupta*	Eurasian	+	+	-	-	-	-
Gramineae	*Arundo donax*	South and central Asia	+	+	-	-	+	+
Gramineae	*Avena barbata*	Mediterranean	+	+	+	native	-	native
Gramineae	*Avena fatua*	Europe	-	+	+	+	-	native
Gramineae	*Avena sterilis*	Mediterranean	-	+	+	native	-	native
Gramineae	*Briza minor*	Southern and western Europe	+	+	+	-	-	-
Gramineae	*Bromus arenarius*	Australia	+	+	-	-	-	native
Gramineae	*Bromus diandrus*	Mediterranean Basin	-	+	-	-	-	-
Gramineae	*Bromus hordeaceus*	Eurasian	+	+	-	-	-	native
Gramineae	*Bromus rubens*	Europe and Mediterranean basin	-	+	-	-	native	native
Gramineae	*Bromus madritensis*	Europe and Mediterranean basin	+	+	-	-	native	native
Gramineae	*Bromus tectorum*	Eurasia and Mediterranean basin	-	+	-	-	-	native
Gramineae	*Bromus trinii*	Western South America	+	+	native	-	-	-
Gramineae	*Bromus willdenowii*	South America	-	+	native	-	-	+
Gramineae	*Cenchrus echinatus*	America s.l.	-	+	native	-	-	-
Gramineae	*Cenchrus incertus*	Neotropical	-	+	-	-	-	-
Gramineae	*Cynodon dactylon*	Warm temp and tropical Old World	+	+	+	+	native	native
Gramineae	*Cynodon transvalensis*	South Africa	-	+	-	-	-	-
Gramineae	*Chloris gayana*	Central and southern Africa	-	+	-	-	-	-
Gramineae	*Chloris virgata*	Warm temp regions worldwide	+	+	native	native	-	-
Gramineae	*Dactyloctenium aegyptium*	Mediterranean and tropical	-	+	+	native	-	-
Gramineae	*Digitaria bicornis*	Asia	-	+	-	-	-	-
Gramineae	*Digitaria ciliaris*	Eurasia and N Africa	-	+	-	-	-	-
Gramineae	*Digitaria sanguinalis*	Eurasia and Mediterranean basin	+	-	+	-	native	native
Gramineae	*Echinochloa colona*	Paleotropical	-	+	+	+	-	-
Gramineae	*Echinochloa crus-galli*	Warm temp and tropical Old World	-	+	-	-	native	native
Gramineae	*Echinochloa hispidula*	Eastern Asia	-	-	-	-	-	+
Gramineae	*Echinochloa oryzicola*	Eastern Asia	-	-	-	-	-	+
Gramineae	*Echinochloa oryzoides*	Eastern Asia	-	-	-	-	-	+
Gramineae	*Eleusine indica*	Paleotropical	+	+	-	-	-	+
Gramineae	*Elymus hispidus*	Eurasia and Mediterranean basin	-	-	-	-	-	-
Gramineae	*Eragrostis barrelieri*	Mediterranean	-	+	-	-	-	native
Gramineae	*Eragrostis cilianensis*	Southern Africa	-	+	+	native	native	native
Gramineae	*Eragrostis curvula*	Southern Africa	+	+	-	+	-	+
Gramineae	*Eragrostis lehmanniana*	Southern Africa	+	+	-	-	-	-
Gramineae	*Eragrostis minor*	Eurasia and northern Africa	-	-	-	-	-	+
Gramineae	*Eragrostis viscosa*	Neotropical	+	+	+	native	native	native
Gramineae	*Eriochloa acuminata*	North America	+	+	-	-	-	-
Gramineae	*Eriochloa contracta*	Central and South United States	-	+	+	-	-	-

Family	Species	Origin						
Gramineae	*Gastridium ventricosum*	Mediterranean basin s.l.	+	+	-	-	-	-
Gramineae	*Holcus lanatus*	Eurasia and Mediterranean basin	+	-	-	-	-	native
Gramineae	*Hordeum distichon*	Irano-turanian	-	-	+	-	-	+
Gramineae	*Hordeum murinum*	Eurasia and Mediterranean basin	-	+	+	native	native	native
Gramineae	*Lamarckia aurea*	Mediterranean	+	native	-	native	native	native
Gramineae	*Lolium perenne*	Eurasia and Mediterranean basin	+	+	-	-	-	-
Gramineae	*Lolium temulentum*	Mediterranean	+	+	-	-	-	-
Gramineae	*Oryza sativa*	Eastern Asia	-	-	-	-	-	+
Gramineae	*Panicum antidotale*	India	+	+	-	-	-	-
Gramineae	*Panicum capillare*	North America	-	-	-	-	-	+
Gramineae	*Panicum dichotomiflorum*	North America	-	-	-	-	-	+
Gramineae	*Panicum miliaceum*	Temperate Asia	-	+	-	-	-	+
Gramineae	*Panicum repens*	Paleotropical	-	-	-	+	-	-
Gramineae	*Paspalum dilatatum*	South America	+	+	-	-	-	-
Gramineae	*Paspalum paspalodes*	Neotropical	-	-	-	-	-	+
Gramineae	*Pennisetum ciliare*	Mediterranean and tropical	+	+	-	+	-	-
Gramineae	*Pennisetum setaceum*	Eastern Africa	+	+	-	-	-	-
Gramineae	*Pennisetum villosum*	Eastern Africa	+	+	-	-	-	+
Gramineae	*Phalaris canariensis*	NW Africa and Canary islands	+	-	+	native	native	-
Gramineae	*Phalaris caroliniana*	Eastern United States	-	+	-	-	-	-
Gramineae	*Phalaris minor*	Mediterranean-irano-turanian	+	+	+	native	native	native
Gramineae	*Phalaris paradoxa*	Europe and Mediterranean basin	+	+	+	-	-	native
Gramineae	*Poa annua*	Eurasian	+	+	+	-	-	native
Gramineae	*Polypogon monspeliensis*	Mediterranean and paleotropical	-	+	+	native	native	native
Gramineae	*Polypogon viridis*	Mediterranean and paleotropical	+	+	+	-	native	native
Gramineae	*Saccharum ravennae*	Eurasia and northern Africa	-	+	-	native	native	native
Gramineae	*Schismus arabicus*	Saharian-arabian	+	+	-	native	native	-
Gramineae	*Schismus barbatus*	Mediterranean-saharian-arabian	+	+	-	native	native	native
Gramineae	*Secale cereale*	Southwestern Asia	+	-	-	-	-	-
Gramineae	*Setaria pumila*	Eurasia and Mediterranean basin	+	+	-	-	-	native
Gramineae	*Setaria verticillata*	Europe and Mediterranean basin	+	+	+	native	native	native
Gramineae	*Setaria viridis*	Eurasian	+	+	-	-	-	native
Gramineae	*Sorghum bicolor*	Tropical Africa	+	+	+	-	-	-
Gramineae	*Sorghum halepense*	Paleotropical	-	+	-	-	+	+
Gramineae	*Tragus racemosus*	Paleotropical	-	+	-	native	native	-
Gramineae	*Triticum aestivum*	Irano-turanian	-	+	-	-	-	+
Gramineae	*Vulpia bromoides*	Europe and Mediterranean basin	+	+	-	-	-	-
Gramineae	*Vulpia myuros*	Europe and Mediterranean basin	+	+	+	-	-	-
Hydrocharitaceae	*Hydrilla verticillata*	Eurasian	+	+	-	-	-	-

Family	Species	Origin						
Hydrocharitaceae	*Egeria densa*	North America	-	-	-	-	-	-
Iridaceae	*Iris germanica*	Unknown	-	-	-	-	-	+
Juncaceae	*Juncus acutus*	Cosmopolitan	-	native	-	native	native	native
Labiatae	*Lamium amplexicaule*	Eurasian	+	+	-	-	native	native
Labiatae	*Marrubium vulgare*	Europe and Mediterranean	+	+	+	-	-	native
Labiatae	*Mentha spicata*	Unknown	+	+	+	-	-	-
Labiatae	*Salvia sclarea*	Irano-turanian	-	-	-	-	-	+
Labiatae	*Stachys arvensis*	Europe and Mediterranean	-	-	+	-	-	-
Leguminosae	*Acacia farnesiana*	Neotropical	-	-	-	-	+	-
Leguminosae	*Acacia saligna*	Australia	-	-	-	-	+	-
Leguminosae	*Alhagi pseudalhagi*	Western Asia	+	+	+	-	-	-
Leguminosae	*Caesalpinia gilliesii*	South America	-	+	+	-	-	-
Leguminosae	*Ceratonia siliqua*	Eastern Mediterranean basin	-	+	+	-	+	-
Leguminosae	*Indigofera suffruticosa*	Neotropical	-	+	+	-	-	-
Leguminosae	*Leucaena leucocephala*	Neotropical	-	+	+	-	-	-
Leguminosae	*Medicago lupulina*	Europe and Mediterranean basin	+	+	+	-	native	native
Leguminosae	*Medicago polymorpha*	Mediterranean s.l.	-	+	+	-	native	-
Leguminosae	*Medicago sativa*	Irano-turanian	+	-	-	-	-	+
Leguminosae	*Melilotus alba*	Eurasian	+	+	+	+	-	native
Leguminosae	*Melilotus indicus*	Mediterranean-irano-turanian	+	+	+	+	native	native
Leguminosae	*Parkinsonia aculeata*	Neotropical	-	-	native	+	+	-
Leguminosae	*Pediomelum rhombifolium*	North America	-	-	-	-	-	-
Leguminosae	*Robinia pseudoacacia*	North America	+	-	-	-	-	+
Leguminosae	*Trifolium repens*	Europe and Mediterranean basin	-	+	+	+	-	native
Leguminosae	*Vicia villosa*	Eastern Europe and western Asia	-	-	-	-	-	+
Liliaceae	*Gasteraloe x beguinii*	South Africa	-	+	-	-	-	+
Liliaceae	*Aloe vera*	Neotropical	+	+	-	-	-	-
Liliaceae	*Asphodelus fistulosus*	Mediterranean	-	+	-	-	-	native
Lythraceae	*Ammannia coccinea*	Neotropical	+	-	-	-	native	+
Lythraceae	*Ammannia robusta*	Neotropical	+	native	-	native	-	+
Malvaceae	*Malva neglecta*	Europe, NW Africa and SW Asia	-	+	-	-	-	native
Malvaceae	*Malva parviflora*	Mediterranean-irano-turanian	+	+	+	native	native	native
Malvaceae	*Malva sylvestris*	Eurasian and Mediterranean	-	-	+	-	native	native
Malvaceae	*Sida spinosa*	Paleotropical	-	-	-	-	-	+
Meliaceae	*Melia azedarach*	Eastern and southern Asia	-	+	+	-	-	-
Molluginaceae	*Glinus lotoides*	Mediterranean and tropical	-	+	+	-	-	-
Molluginaceae	*Glinus radiatus*	Neotropical	-	+	+	-	-	-
Molluginaceae	*Mollugo cerviana*	Mediterranean and tropical	+	+	+	native	-	-
Moraceae	*Ficus carica*	Eastern Mediterranean basin	-	-	-	+	+	+

Family	Species	Origin	1	2	3	4	5	6
Moraceae	Maclura pomifera	North America	-	-	-	+	-	-
Myrtaceae	Eucalyptus camaldulensis	Australia	-	+	-	+	-	-
Nyctaginaceae	Boerhavia diffusa	Pantropical	+	-	+	+	-	-
Nyctaginaceae	Mirabilis jalapa	Neotropical	-	-	+	+	+	-
Onagraceae	Oenothera drummondii	North America	-	-	+	-	+	-
Onagraceae	Oenothera laciniata	Eastern United States	+	-	+	+	+	native
Oxalidaceae	Oxalis corniculata	Old World	+	native	+	+	+	-
Oxalidaceae	Oxalis pes-caprae	South Africa	+	+	native	+	+	native
Palmae	Phoenix dactylifera	Saharo-arabian	native	-	+	-	+	-
Papaveraceae	Argemone ochroleuca	Western and central Mexico	-	-	-	+	+	native
Papaveraceae	Glaucium corniculatum	Mediterranean-irano-turanian	-	-	native	+	-	native
Papaveraceae	Fumaria capreolata	Mediterranean s.l.	native	native	native	-	+	native
Papaveraceae	Fumaria officinalis	Mediterranean s.l.	native	-	+	+	-	+
Papaveraceae	Fumaria parviflora	Mediterranean s.l.	-	-	+	+	-	native
Papaveraceae	Papaver dubium	Eurasia and northern Africa	-	+	+	-	-	native
Papaveraceae	Papaver somniferum	Eastern Mediterranean basin	+	native	+	+	+	native
Pedaliaceae	Sesamum orientale	Paleotropical	-	-	-	+	-	-
Pinaceae	Pinus halepensis	Mediterranean	-	-	+	-	-	native
Plantaginaceae	Plantago lanceolata	Eurasia and Mediterranean bassin	+	native	+	+	+	native
Plantaginaceae	Plantago major	Europe and Mediterranean basin	-	+	+	+	native	native
Polygonaceae	Polygonum argyrocoleon	Saharian-arabian	native	native	+	+	native	-
Polygonaceae	Polygonum arenastrum	Cosmopolitan	-	-	+	+	-	native
Polygonaceae	Polygonum aviculare	Cosmopolitan	-	native	+	+	-	native
Polygonaceae	Polygonum persicaria	Cosmopolitan	-	-	+	+	-	native
Polygonaceae	Rumex conglomeratus	Europe, N Africa, C and W Asia	native	native	+	+	native	-
Polygonaceae	Rumex obtusifolius	Europe and W Asia	native	native	+	+	-	native
Polygonaceae	Rumex pulcher	Eurasian	native	native	+	+	-	native
Polygonaceae	Rumex crispus	Cosmopolitan	native	native	+	+	native	-
Pontederiaceae	Eichhornia crassipes	Neotropical	-	-	+	-	-	-
Pontederiaceae	Heteranthera limosa	Neotropical	-	-	-	-	+	-
Pontederiaceae	Heteranthera reniformis	Neotropical	-	+	-	-	+	+
Pontederiaceae	Heteranthera rotundifolia	Neotropical	-	+	-	-	+	native
Portulacaceae	Portulaca oleracea	Cosmopolitan	+	native	+	+	+	native
Primulaceae	Anagallis arvensis	Europe, W. Asia and N. Africa	+	native	+	+	+	-
Punicaceae	Punica granatum	Irano-turanian	-	+	-	-	-	-
Ranunculaceae	Nigella sativa	Eastern Asia	+	-	-	-	-	-
Rosaceae	Prunus dulcis	Irano-turanian	-	-	+	-	-	+
Rubiaceae	Galium aparine	Europe and Mediterranean	+	-	+	+	native	native
Rubiaceae	Sherardia arvensis	Eurasian and Mediterranean	+	native	+	+	native	native

Family	Species	Origin						
Rutaceae	*Ruta chalepensis*	Mediterranean basin	-	-	-	-	native	native
Salicaceae	*Populus euphratica*	Central and southwesterm Asia	-	+	-	-	-	-
Salviniaceae	*Salvinia molesta*	Brazil	-	+	-	-	-	-
Scrophulariaceae	*Bacopa monnieri*	Tropical s.l.	-	+	-	-	-	-
Scrophulariaceae	*Lindernia dubia*	North America	-	-	-	-	-	+
Scrophulariaceae	*Veronica anagallis-aquatica*	Eurasia and northern Africa	+	native	-	-	-	native
Scrophulariaceae	*Veronica arvensis*	Eurasian and Mediterranean	+	-	-	-	-	native
Scrophulariaceae	*Veronica persica*	Southwestern Asia	+	-	+	-	+	+
Simaroubaceae	*Ailanthus altissima*	China	-	-	-	-	-	+
Solanaceae	*Calibrachoa parviflora*	South America	+	-	-	-	-	-
Solanaceae	*Datura innoxia*	Central America and Mexico	+	+	+	-	+	+
Solanaceae	*Datura metel*	Neotropical	-	-	-	-	-	-
Solanaceae	*Datura stramonium*	America s.l.	+	-	-	-	+	+
Solanaceae	*Lycopersicon esculentum*	Central and South America	-	-	native	-	+	-
Solanaceae	*Nicotiana glauca*	South America	+	+	-	native	+	-
Solanaceae	*Physalis pubescens*	Eastern United States	+	+	-	-	+	-
Solanaceae	*Solanum americanum*	South America	+	+	-	-	-	-
Solanaceae	*Solanum elaeagnifolium*	South America	+	+	-	-	-	-
Solanaceae	*Solanum nigrum*	Eurasian and Mediterranean	-	-	+	-	native	native
Solanaceae	*Solanum triflorum*	South America	+	-	-	-	-	-
Tamaricaceae	*Tamarix aphylla*	From Africa to India	+	+	+	native	-	-
Tamaricaceae	*Tamarix chinensis*	Eastern Asia	+	+	-	-	-	-
Tamaricaceae	*Tamarix gallica*	Mediterranean-saharian-arabian	+	-	native	native	native	native
Tamaricaceae	*Tamarix parviflora*	Eastern Mediterranean basin	+	+	-	-	+	-
Tamaricaceae	*Tamarix ramosissima*	Eastern Asia	+	+	-	-	+	-
Ulmaceae	*Celtis australis*	Eastern Mediterranean basin	-	-	-	-	-	+
Ulmaceae	*Ulmus parviflora*	China and Japan	+	+	-	-	+	-
Ulmaceae	*Ulmus pumila*	Central Asia	+	-	-	-	-	-
Umbelliferae	*Ammi visnaga*	Mediterranean-irano-turanian	-	+	+	-	-	native
Umbelliferae	*Anethum graveolens*	Eastern Mediterranean basin	+	-	-	-	-	-
Umbelliferae	*Apium graveolens*	Eurasian	-	+	+	-	-	-
Umbelliferae	*Coriandrum sativum*	North Africa and west Asia	+	+	-	-	-	-
Umbelliferae	*Cyclospermum leptophyllum*	Brazil	+	+	-	-	-	-
Umbelliferae	*Torilis nodosa*	Mediterranean	+	-	-	-	-	native
Urticaceae	*Urtica urens*	Cosmopolitan	+	+	+	native	native	native
Verbenaceae	*Lippia nodiflora*	Tropical s.l.	native	-	native	-	-	-
Zygophyllaceae	*Kallstroemia parviflora*	Southern USA and Mexico	+	-	-	+	-	-
Zygophyllaceae	*Tribulus terrestris*	Eurasia and northern Africa	+	native	+	native	native	native
Zygophyllaceae	*Zygophyllum fabago*	Irano-turanian	+	+	-	+	+	+

Table 2
Tests of significance for dependent variable (invasiveness) and predictors which are significantly related.
Sigma-restricted parameterization. Effective hypothesis decomposition.

	Sum of squares	df	Mean-square	*F*-ratio	*p*-value
Intercept	425.0527	1	425.0527	1736.809	0.000000
Dispersal syndrome	2.8062	3	0.9354	3.822	0.010232
Error	83.9431	343	0.2447		
Intercept	620.3791	1	620.3791	2514.645	0.000000
Linking to disturbed sites	1.6356	1	1.6356	6.630	0.010446
Error	85.1137	345	0.2467		

arid areas shows that, in general, the dry areas of the Old World are more distinct than those of the American continent (Table 3).

DISCUSSION AND CONCLUSIONS

Our approach enables us to identify the factors that favour the invasiveness of introduced species in arid zones. Until now, only a few species attributes have been shown to be significantly related to the invasiveness of alien plants (THOMPSON & *al*., 1995; SOBRINO & *al*., 2002; LLORET & *al*., 2003; SANZ ELORZA & *al*., 2006). The two predictors that we have found to be related to the phenomenon in dry areas had already been related to the invasiveness of alien species in other parts of the world, and in other ecological environments. The relation between dispersal syndrome and invasion success of the species dispersed by wind (anemochorous) in the western Mediterranean (GASSÓ & *al*., 2009) has been proved and coincides with what has been observed in dry areas. Nevertheless, in these dry areas, species dispersed by water (hydrochorous) have also shown themselves to be capable of becoming successful invaders. Obviously, in dry areas the environments where hydrochorous species can trigger invasion processes are very limited, therefore resulting in surface extension areas which are not very significant. Moreover, in specific concrete and delimited wetland habitats the application of prevention and control strategies is much more straightforward. On the other hand, species linked to moist soils have not shown themselves to be more efficient invaders in any

significant way, although in areas where agriculture with irrigation is important the opposite may be true. This situation occurs in Monegros (Table 3), and is the explanation for the different behaviour of this area with respect to the general pattern. Many of the invasive alien species present are weeds of irrigated crops that come from tropical areas (SANZ ELORZA & *al*., 2006).

Apart from dispersal syndrome and linking to disturbed sites, the rest of the traits studied have not been found to be related to invasion success. It is striking that characteristics such as seed size, capacity for clonal reproduction, linking to moist soils or longevity do not explain the phenomenon of invasiveness of alien plants in dry areas, as could have at first been assumed. This situation reinforces the theory of the absence of a general pattern of the attributes of invasive species, as these are largely dependent on the type of habitat and the geographical environment in which they are found (THOMPSON & *al*., 1995).

In the comparison of the alien flora of the six areas studied (Table 3), it can be seen that the Tabernas Desert differs significantly in all the attributes with respect to the global pattern of the arid areas. Monegros is only 700 km away, and is only significantly different with respect to linking to moist soils due to the importance of irrigated agriculture. The attributes of the alien flora of Monegros seem to bear a closer resemblance to the alien flora of the deserts of North America, where the arid conditions are more similar and not as extreme as those of the Sahara or the Atacama and Peruvian Deserts. These last two, which are the most genuine deserts, show significant differences in biological types, with a gre-

Table 3

Percentages of the number of alien species present in each area studied and in all the areas as a whole, for each of the predictors taken into account. The biological types are: C chamaephyte, G geophyte, H hemicryptophyte, Hy hydrophyte, P phanerophyte, T therophyte. The pollination modes are: An anemophilous, En entomophilous, Hi hydrophilous. The dispersal syndromes are: An wind (anemochorous), Hi water (hydrochorous), Zoo animals (zoochorous), others (including barochorous, balistochorous, etc.). The test χ^2 was used to determine if significant differences exist between the results obtained in each of the areas.

		Mojave	Sonoran Desert	Atacama	Sahara	Tabernas	Monegros	Global
Biological type	C	3	3	2	0	9	3	3
	G	4	4	7	5	6	4	4
	H	18	15	12	19	13	11	45
	Hy	3	3	7	10	0	7	3
	P	15	13	0	0	38	10	13
	T	59	62	72	67	34	65	62
	χ^2	1.0528	0.0931	23.1296	34.0532	-	7.2375	-
	p-value	0.9582	0.9998	0.0003	< 0.0001	< 0.0001	0.2036	-
Clonality	no	79	82	85	74	66	79	80
	yes	21	18	15	26	34	21	20
	χ^2	0.0625	0.2500	1.5625	2.2500	12.2500	0.0625	-
	p-value	0.8026	0.6171	0.2113	0.1336	0.0005	0.8026	-
Linked to moist soils	no	51	54	48	48	62	44	52
	yes	49	46	52	52	38	66	48
	χ^2	0.0401	0.1603	0.6410	0.6410	4.0064	7.9807	-
	p-value	0.8414	0.6889	0.4234	0.4234	0.0453	0.0047	-
Pollination mode	An	71	69	77	67	47	68	66
	En	28	30	23	33	53	32	33
	Hi	1	1	0	0	0	0	1
	χ^2	1.1363	0.4091	5.8636	1.0152	18.5909	1.0909	-
	p-value	0.5665	0.8150	0.0533	0.6019	< 0.0001	0.5796	-
Dispersal syndrome	An	50	38	34	29	19	28	35
	Hi	1	4	2	5	0	10	5
	Zoo	13	19	21	12	25	21	19
	others	36	38	43	55	56	42	41
	χ^2	12.1331	0.6766	2.1366	8.3881	19.6968	6.6349	-
	p-value	0.0069	0.8787	0.5445	0.0386	0.0002	0.0845	-
Seed size	VS	25	20	18	31	19	17	20
	S	39	44	51	50	28	43	44
	M	14	16	10	10	19	26	15
	L	14	14	13	5	28	10	13
	VL	9	7	8	5	6	4	7
	χ^2	2.5332	0.1436	3.1232	14.0294	24.3854	10.5174	-
	p-value	0.6387	0.9975	0.5374	0.0072	< 0.0001	0.0326	-
Linked to distubed sites	no	30	28	21	26	47	21	29
	yes	70	72	79	76	53	79	71
	χ^2	0.0456	0.0455	3.1033	0.6625	15.7358	3.1083	-
	p-value	0.8256	0.8257	0.0779	0.4157	< 0.0001	0.0779	-
Salinity tolerance	no	84	91	92	88	84	94	91
	yes	16	9	8	12	16	6	9
	χ^2	5.9829	-	0.1221	1.0989	5.9829	1.0989	-
	p-value	0.0144	1	0.7268	0.2945	0.0144	0.2945	-
Longevity	annual	59	64	72	69	38	69	63
	perenne	41	36	28	31	62	31	37
	χ^2	0.6864	0.0429	3.4749	1.5444	-	1.5444	-
	p-value	0.4074	0.8359	0.0623	0.2139	<0.0001	0.2139	-

ater presence of therophytes and an almost total absence of phanerophytes and chamaephytes. This is easily explained if we consider the conditions of extreme dryness of these deserts and the absence of wetlands and fluvial courses that could mitigate the situation on a local scale. In these conditions, the therophytes are the best adapted to survive, as they take advantage of any sign of temporary humidity that allows them to complete their cycle quickly. In the alien flora of the Sahara, significant differences can be observed in the global pattern of seed size, as the species with small seeds acquire greater quantitative importance. Many of the alien species in the Sahara are, in fact, therophytes of Mediterranean origin with small seed size. The Sonoran Desert does not significantly differ from the general pattern in any of the traits we considered. This is partly because this zone had the greatest number of alien species of all the arid zones in the study. This could be because there are more environments which are altered by human influence, as there are several cities with large populations in this desert, unlike in the other five areas. In the Mojave Desert, the significant difference which can be seen with respect to dispersal syndrome is worth noting. This is caused by the greater fre-

quency of alien species with anemochorous dispersion.

We can conclude that in dry areas, dispersal syndrome is a determining factor of invasiveness. This agrees with the descriptions in the classic literature about the ecology of invasive alien plants (RICHARDSON & *al*., 2000; KOLAR & LODGE, 2001; PRINZING & *al*., 2002). Moreover, the harsh environmental conditions of the arid zones create an ecological barrier that is difficult for alien plants to overcome, as they tend to be concentrated in environments which are altered by human activity. For this reason, the best preventative measure against invasive alien plants has been shown to be making the preservation of the habitats of arid zones a priority in nature conservation policies. The differences in the attributes of the alien species in the six areas studied show that, in spite of the fact that they all have an arid climate in common, there are more subtle environmental factors in play which cause deviations with respect to a hypothetical general situation. Therefore, the theory of the absence of a general pattern in the attributes of alien species is proved to be true. These species are largely dependent on local conditions, even in the case of regions with major climatic analogies.

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