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Invasive alien plants in China: role of clonality and geographical origin

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Abstract

Biological invasions have become a significant threat to the global environment. Unfortunately, to date there is no consensus on invasion mechanisms and predictive models. Controversies range from whether we can reliably predict which species may become invasive to which species characteristics (e.g., life history, taxonomic groups, or geographic origin) contribute to the invasion processes. We examined 126 invasive alien plant species in China to understand the role of clonality and geographical origin in their invasion success. These species were categorized into three groups (I, II, III) based on their invasiveness in terms of current spatial occupation and the degree of damage to invaded habitats. Clonal plants consisted of almost half (44%) of the 126 invasive species studied, and consisted of 66% of 32 the most invasive alien plant species (Group I). There was a significant positive relationship between clonality and species invasiveness. A 68% of the 126 species studied originated in the continent of America (North and/or South America). These preliminary findings support that America is the primary geographical origin of invasive alien plant species in China and that clonality of the invasive plant species contributed significantly to the their invasiveness. The results suggest an urgent need at the global scale to investigate the mechanisms whereby plant clonal growth influences plant invasions, and the need for a focus at regional scale to examine factors affecting the exchange of invasive plant species between America and China.

Introduction

Plant invasion has become a significant threat to biodiversity, environment and economies both globally and locally (Mack et al. 2000; Pimentel et al. 2000; Liu et al. 2001; Mitchell and Power 2003). It is critical to analyze the invasive ability of alien plants before introduction so that likely invasive species can be screened (Goodwin et al. 1999). Thus, two of the urgent tasks of ecologists who are investigating biological invasions are to understand the factors influencing invasion success of plants and to develop means to predict plant invasions (Heger and Trepl 2003). Unfortunately, to date there is no consensus on invasion mechanisms and predictive models (Alpert et al. 2000; Milbau

et al. 2003). Controversies range from whether we can reliably predict which species may become invasive to which species characteristics (e.g., life history, taxonomic groups, or geographic origin) contribute to the invasion processes.

Clonality, an important trait enhancing plants' exploitation of ubiquitous environmental heterogeneity, may aid plants to invade new habitats (Maurer and Zedler 2002). Also, clonality can contribute to spatial occupation at a local scale and risk spreading of the clonal plants (Dong 1996b). Asexual clonal reproduction is one of the characters of some highly invasive plants (Baker 1974; Sakai et al. 2001). A considerable number of invasive plant species have the capability of vigorous clonal propagation and their invasiveness maybe related to clonality (Leakey 1981; Dong 1996a; Rejmánek 1999; Kolar and Lodge 2001). Yet, we found few studies to support this conclusion quantitatively.

The geographical origin of alien species may influence their invasiveness in new areas (Reichard 2001; Lloret et al. 2004). In addition, species from a large continent may more easily invade a new habitat where the climate is similar to their geographical origin, as compared to species from a small continent and in new habitat having a different climate (Mihulka and Pyšek 2001). Successful invaders mainly originate from large continents with diverse biota (Sax and Brown 2000). China is the third largest country in the world in terms of territory and possesses mega-diversity of plant species with numerous invasive alien plant species (Xie et al. 2000). However, there are a few quantitative analysis of geographic origin for invasive species in China.

In this study, we analyzed characters of 126 major invasive alien plant species in China, including plant traits such as clonality, life form, and geographic origin to understand the role of clonality and geographical origin in their invasion success.

Methods

Data collection

So far, a few researchers have published different lists of invasive alien plants existing in China. For instance, 58, 90 and 80 invasive alien plant species were reported by Ding and Wang (1998), Li and Xie (2002) and Xiang et al. (2002), respectively. We integrated the data from those three lists according to the definition of invasive plants by Richardson et al. (2000) and Pyšek et al. (2004), i.e., ''invasive plants are a subset of naturalized plants that produce reproductive offspring, often in very large numbers, at considerable distances from the parent plants, and thus have the potential to spread over a large area''. We removed the overlapping species and corrected wrong records. As a result, a new list containing 126 major invasive plant species was derived and used for the present study. We extensively consulted published literature for the data of each of the species (Editorial Board for Flora of China 1959~2002; Li 1998; Li and Xie 2002). Data from literature were used to construct a detailed database for the plant species under study, including characters such as invasiveness, plant traits, provincial distribution and geographic origin. The geographic origin in our study refers to evolutionary origin where the plant species evolved as a native species.

Data analyses

A geographic distribution map, based on the number of invasive plant species, was made according to the distribution information listed in our detailed database using Arcview GIS 3.2. Plant traits that can be identified and used easily were chosen (Reichard 2001). The traits selected in this study were clonality, life form, geographical origins, provincial distribution and invasiveness. Based on clonality, the plants were divided into clonal plants, with different types of clonal organs and non-clonal plants; while based on life form, the plants were categorized as annual and perennial herbs and shrubs. The geographical origins included America, Europe, Africa and Asia. In general it is difficult to determine the invasiveness of a species, however we evaluated plants' invasiveness in terms of their current spatial occupation and impacts that can be obtained from literature.

The 126 species were divided into three groups. The invasiveness decreases from group I, group II to group III. The first group (Group I) consists of

those species that occupied extensive areas and/or with severe damage to local diversity. These species have all been listed in the books *100 of the World's Worst Invasive Alien Species* (IUCN 2001) and/or *The World's Worst Weeds* (Holm et al. 1977), except for *Eupatorium adenophorum* and *Alternanthera philoxeroides*, which have been recorded recently as notorious invasive alien plants in China (Li and Xie 2002). The second group (Group II) includes those species that occupied large area (>300 km^2) and/or had strong negative influence. The third group (Group III) contains those species that occupied a relatively small area and/or had relatively small harmful impacts. According to the habitats the plants invaded, the 126 invasive alien plant species in China were also divided into the following categories: natural area invaders inhabiting areas experiencing slight human disturbance (e.g. forest and wetland); non-natural area invaders inhabiting areas experiencing strong human disturbance (e.g. roadside and cropfield); and invaders of both areas (Daehler 1998; Li 1998; Li and Xie 2002). Spearman's correlations were made for all the characters using SPSS (SPSS for Windows, Rel. 10.0.1, 1999, Standard Version).

Results

Clonality and invasiveness

Based on Ding and Wang (1998), Li and Xie (2002) and Xiang et al. (2002), a total of 126 major alien invasive species in China was studied for their clonality, life form, geographic origin and invasiveness (Appendix A). The number of invasive plant species decreases towards more western and northern China (Figure 1). Over 60% of these species invaded non-natural areas (Figure 2).

These species showed different degrees of invasion success at the time of the investigation. Approximately 25% of the 126 species were the

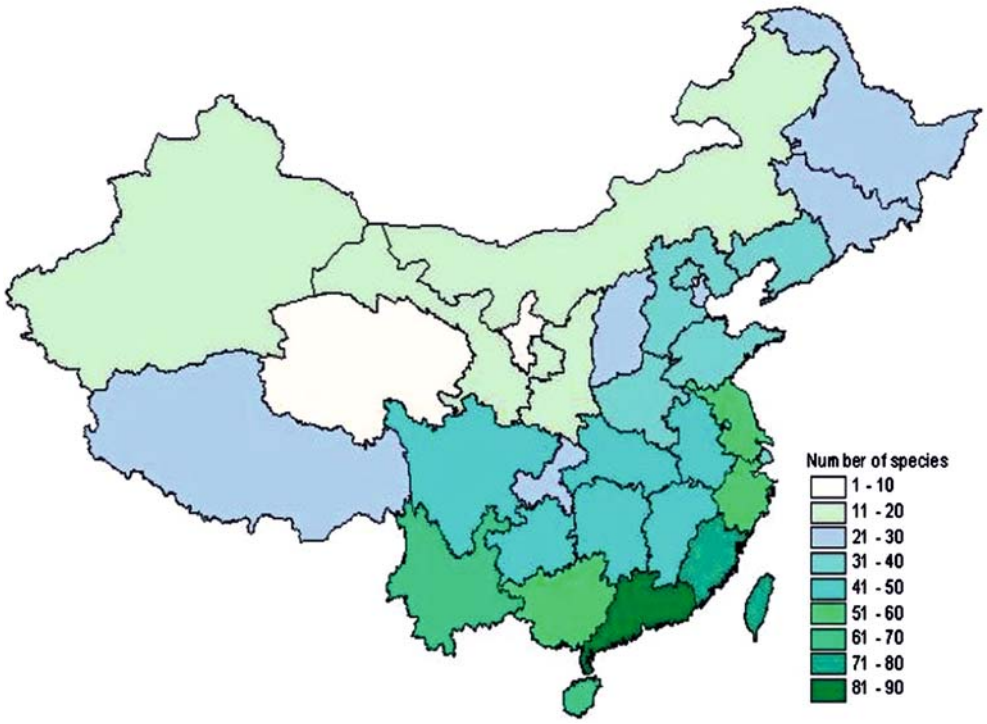

Figure 1. The provincial distribution of the 126 invasive alien plant species in China. The species richness of invasive plants in every provincial administrative unit was collected according to the distribution information. Arcview GIS 3.2 was used for the figure of the distribution pattern. The color codes represent the number of species in each province.

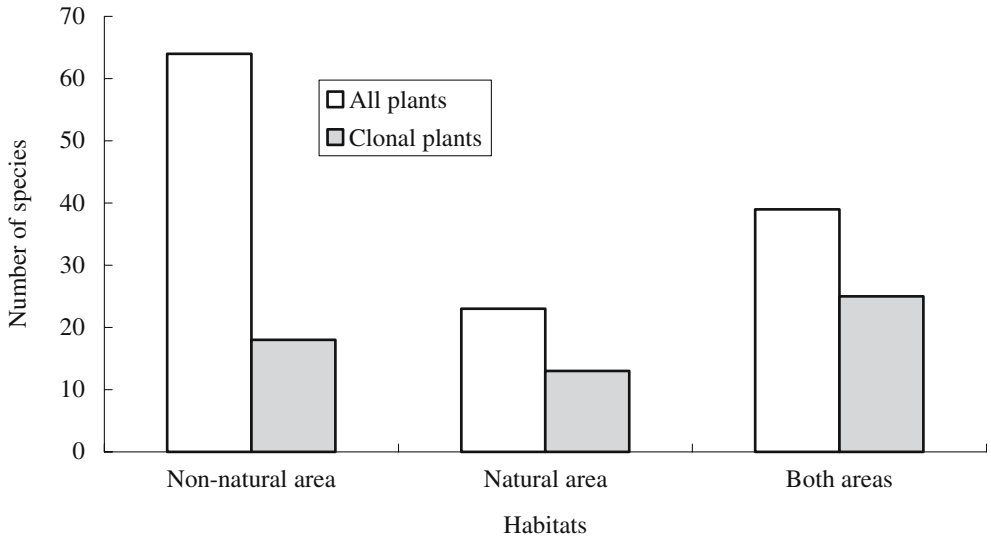

Figure 2. The number of clonal plants found in different habitats including natural areas (forests and wetlands with relatively low human disturbance), non-natural area (crop-lands and roadsides with relatively high human disturbance), and both natural and non natural areas.

most invasive species (Group I); 31% were those with invaded area >300 km^2 (Group II) exhibiting strong negative influence in the invaded area; and 43% made as the third group (Group III) containing species that occupied relatively small area and/or had relatively small harmful impact.

Clonal plants consist of almost half (44%) of the 126 species, including 17% with rhizomes, 11% with stolons, 11% with tillers and 14% with other clonal organs (e.g. tubers and/or bulbs) (Table 1). Some clonal plants had more than one type of clonal organ. For example, *Alternanthera philoxeroides* uses stolons and storage roots and *Cyperus rotundus* uses rhizome and tubers for propagation. Clonal plants accounted for 66% of 32 most invasive species (Group I). A significant positive correlation between clonality and invasiveness ($P < 0.05$, based on the 126 species) was identified by the Spearman's correlation analyses (Table 2). In particular, clonal species with stolon and tiller showed significant correlations with invasiveness. While only 28% of the clonal plants were found in the non-natural area invaders, 56% were found in the natural areas and 64% were found in both areas (Figure 2).

Plant life form and invasiveness

Herbaceous species (both perennial and annual) accounted for 88% of the 126 alien invasive species, whereas shrub species was about 11%

Table 1. Analyses of the degree of invasiveness and clonality of 126 invasive alien plant species in China.

Invasiveness	Total #	Clonal plants				
		Total #	No. of species with rhizome	No. of species with stolons	No. of species with tillers	No. of species with other types of clonal organs
Group I	32	21	8	7	9	3
Group II	39	18	5	5	2	7
Group III	55	17	9	2	3	8
Total	126	56	22	14	14	18

Note: A plant species can have multiple clonal organs.

Table 2. Summary of Spearman's correlation analyses based on clonality and life form for 126 invasive alien plant species in China.

r		Invasiveness	Clonality	Clonal organs			Life forms		
				Rhizome	Stolon	Tiller	Other	Annual	Perennial
Invasiveness									
Clonality		0.28*							
Clonal organs	Rhizome	0.07^{ns}	0.51*						
	Stolon	0.24*	0.40*	-0.16^{ns}					
	Tiller	0.25*	0.40*	0.17^{ns}	-0.12^{ns}				
	Others	-0.05^{ns}	0.46*	0.06^{ns}	0.14^{ns}	-0.14^{ns}			
Life forms	Annual	0.07^{ns}	-0.23^{ns}	-0.15^{ns}	-0.11^{ns}	-0.01^{ns}	−0.22*		
	Perennial	-0.05^{ns}	0.28*	0.22*	0.19*	0.09^{ns}	0.14^{ns}	−0.79*	
	Shrub	-0.03^{ns}	-0.08^{ns}	-0.10^{ns}	-0.13^{ns}	-0.13^{ns}	0.13^{ns}	−0.32*	−0.33*

* = $P < 0.05$; ns = Not significant.

(Table 3). Although perennial and annual herbs showed a similar ratio, among the 126 species, 45% and 42%, respectively, the former had 2 times more clonal plants than the latter (60% vs. 31%) (Table 3).

Geographic origin of the invasive species

As high as 68% of the 126 invasive plants species originated in America (North/South) (Table 4). Species with European origin accounted only 18% and Africans and Asian origin was the lowest, 3%. Similarly, species with American origination contributed the highest percentage (22 out of 32 species) for the most invasive species group (Group I). American origin species showed the highest percent (25) of clonal plants, whereas only 10%, 5% and 4% clonal plants were from Europe, Africa and Asia, respectively (Figure 3).

Discussions

Our analyses showed that clonality might play an important role in the invasion process and success for alien species studied in China. Almost half of the species studied and over 60% of the most invasive species (Group I) are clonal plants. Moreover, there was a significantly positive correlation between clonality and the invasiveness. These findings provide new evidence linking clonality to plant invasion, which is in accordance with previous studies based on individual species. For example, Pyšek et al. (2003) found that novel hybrid invasive genotypes may be produced by rare sexual reproduction, fixed by clonal growth, and presents a previously unknown threat to native vegetation. Maurer and Zedler (2002) suggested that both the resource subsidy from parent clones and resource foraging plasticity contribute to invader's ability to spread rapidly into native vegetation. Reichard and Hamilton (1997) studied the invasive plants of America and also found that clonality may enhance invasion. However, the field study of *Populus tremuloides* by Peltzer (2002) showed that clonal integration tended to improve ramet survival and growth, but these trends were often not significant in the species. The relationship between

Table 3. Analyses of invasive alien plant species with different life forms in China.

Life form	Total #	Clonal plants				
		Total #	Rhizome	Stolon	Tiller	Others
Annual	54	17	6	4	6	3
Perennial	57	34	15	10	8	11
Shrub	15	5	1	0	0	4

Note: A plant species can have multiple clonal organ.

Table 4. Analyses of geographic origins of 126 invasive alien plant species in China.

Invasiveness	America	Europe	Africa	Asia
Group I	22	6	2	2
Group II	25	7	4	3
Group III	39	10	4	2
Total	86	23	10	7

clonality and invasiveness in plants may be species specific.

Plants with high invasiveness are often very adaptive. They may displace the native species through competition (Chittka and Schurkens 2001). Clonal plants are regarded as being especially adaptive in heterogeneous environments and contribute greatly in most ecosystems (Hutchings and de Kroon 1994; Dong 1996a; Song et al. 2002). Their adaptive advantages are mainly due to their genetic risk spreading via cloning (Cook 1985; Dong 1996b), intraclonal sharing of resources (Peltzer 2002), foraging behavior (Hutchings and de Kroon 1994; Dong 1996a) and division of labor in clone (Alpert and Stuefer 1997) in spatially heterogeneous (patchy) habitats. Compared to non-clonals, clonal invaders appear to suffer a disadvantage in the dispersal phase of invasion because ramets are usually not able to disperse to great distance (Pyšek 1997). However, most clonal plants possess both asexual (clonal) propagation and sexual reproduction (Eckert 2002) and allocation to both modes may be plastic. For instance, several notorious plant invaders, such as *Mikania micrantha*, *Eupatorium adenophorum*, combine sexual reproduction with strong clonal propagation, (Huang et al. 2000; Song and Dong 2002).

The present study also suggested that America was the primary geographical origin of most invasive alien plant species in China. Asia and North America share a wide range of similar environments and related biota, which may result in each region being more susceptible to each other's immigrant species than species from many other parts of the world (Guo 1999, 2002). Moreover, exchanges of alien plants and animals across the Pacific Ocean are increasing markedly as commerce between these two regions has soared in the past few decades; the rate of these species exchanges will undoubtedly accelerate. Thus, there is an urgent need at the global scale to investigate the mechanisms whereby plant clonal growth influences plant invasions, and the need to focus at regional scale to examine factors affecting the exchange of invasive plant species between America and China.

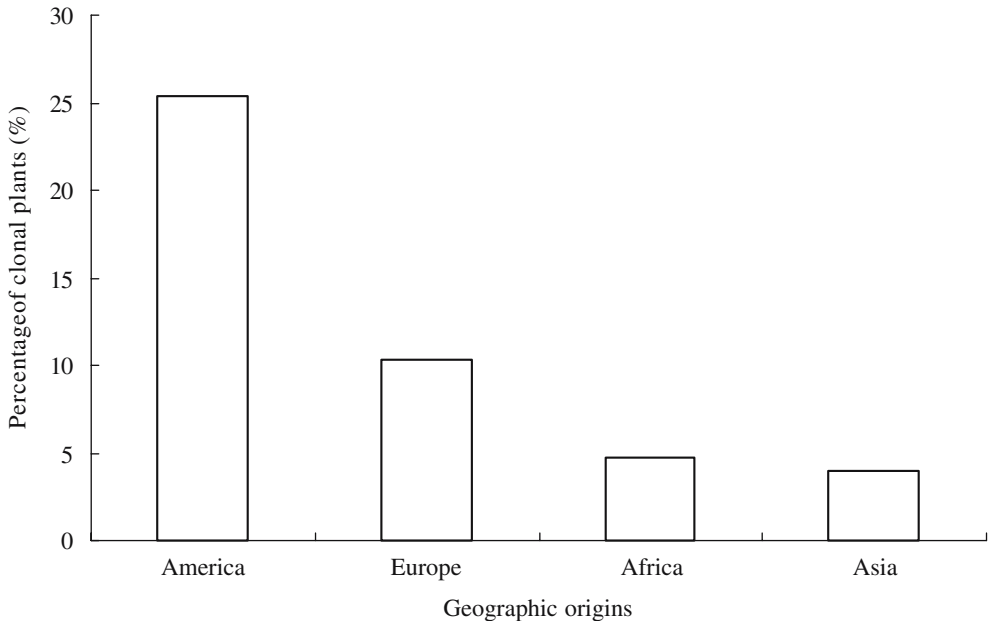

Figure 3. Percentage of clonal plant species based on geographic origins for the 126 invasive alien plant species in China.

Our results revealed a trend of provincial distribution of invasive alien plant species in China that the number got less towards more western and northern places. This illustrates widely the occurrence of invasive alien plants in China and implicates a correlation of plant invasion to the degree of development of economy and society because in general the degree is higher, in addition to national conditions is more favorable for plants, in more eastern and southern places in China.

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Appendix A

Table A1. Checklist of 126 invasive plants in *P.R.* China and their clonality, life forms, geographic origins, and invasiveness.

Species	Clonality	Life forms	Geographic origins	Invasiveness
Acacia farnesiana	No	Shrub	America	Group III
Acanthospermum australe	No	Annual	America	Group III
Ageratum conyzoides	No	Annual	America	Group I
Agrostemma githago	No	Annual	Europe	Group II
Alternanthera philoxeroides	Yes	Perennial	America	Group I
Alternanthera pungens	Yes	Annual	America	Group II
Amaranthus albus	No	Annual	America	Group II
Amaranthus chlorostachys	No	Annual	America	Group III
Amaranthus polygonoides	No	Annual	America	Group II
Amaranthus retroflexus	No	Annual	America	Group II
Amaranthus spinosus	No	Annual	America	Group I
Amaranthus viridis	No	Annual	Africa	Group II
Ambrosia artemisiifolia	No	Annual	America	Group II
Ambrosia trifida	No	Annual	America	Group III
Anredera cordifolia	Yes	Perennial	America	Group II
Apium leptophyllum	No	Annual	America	Group III
Aster subulatus	Yes	Annual	America	Group II
Avena fatua	Yes	Annual	Europe	Group I
Axonopus compressus	Yes	Perennial	America	Group I
Bidens frondosa	No	Annual	America	Group III
Bidens pilosa	No	Annual	America	Group I
Cabomba caroliniana	Yes	Perennial	America	Group II
Cenchrus echinatus	Yes	Annual	America	Group I
Chenopodium ambrosioides	No	Perennial	America	Group II
Chenopodium hybridum	No	Annual	Europe	Group II
Conyza bonarinisis	No	Annual	Europe	Group III
Conyza canadensis	No	Annual	America	Group II
Conyza sumatrensis	No	Perennial	America	Group III
Coreopsis tinctoria	No	Annual	America	Group III
Coronopus didymus	No	Perennial	America	Group II
Crassocephalum crepidioides	No	Annual	Africa	Group II
Cyperus rotundus	Yes	Perennial	Asia	Group I
Datura stramonium	No	Annual	America	Group II
Daucus carota	No	Perennial	Asia	Group III
Eichhornia crassipes	Yes	Perennial	America	Group I
Eleusine indica	Yes	Annual	Asia	Group I

Table A1. Continued.

Species	Clonality	Life forms	Geographic origins	Invasiveness
Erigeron annuus	Yes	Annual	America	Group I
Erigeron philadelphicus	No	Perennial	America	Group III
Eryngium foetidum	No	Perennial	America	Group III
Eupatorium adenophorum	Yes	Shrub	America	Group I
Eupatorium catarium	No	Annual	America	Group II
Eupatorium odoratum	Yes	Perennial	America	Group I
Euphorbia dentata	No	Annual	America	Group III
Euphorbia helioscopia	No	Perennial	America	Group II
Euphorbia hirta	No	Annual	Africa	Group I
Euphorbia maculata	Yes	Annual	America	Group II
Galinsoga parviflora	No	Annual	America	Group I
Geranium carolinianum	No	Perennial	America	Group III
Gomphrena celosioides	No	Annual	America	Group III
Helenium autumnale	No	Perennial	America	Group III
Heliotropium europaeum	No	Annual	Europe	Group III
Hibiscus trionum	No	Annual	Africa	Group II
Hyptis rhomboidea	No	Annual	America	Group III
Hyptis suaveolens	No	Annual	America	Group III
Ipomoea cairica	Yes	Perennial	America	Group III
Ipomoea purpurea	No	Perennial	America	Group II
Lantana camara	No	Shrub	America	Group I
Lemna trinervis	Yes	Perennial	America	Group II
Lepidium campestre	No	Perennial	Europe	Group III
Lepidium perfoliatum	No	Perennial	Europe	Group III
Lepidium virginicum	No	Perennial	America	Group II
Leucaena leucocephala	No	Shrub	America	Group I
Lolium multiflorum	Yes	Annual	Europe	Group II
Lolium temulentum	Yes	Annual	Europe	Group I
Macfadyena unguis-cati	Yes	Shrub	America	Group III
Malvastrum coromandelianum	Yes	Perennial	America	Group III
Melilotus albus	No	Perennial	Europe	Group II
Mikania micrantha	Yes	Perennial	America	Group I
Mimosa invisa	No	Shrub	America	Group I
Mimosa invisa var.*inermis*	No	Shrub	Asia	Group III
Mimosa pudica	No	Shrub	America	Group I
Mirabilis jalapa	Yes	Annual	Africa	Group II
Nasturtium officinale	Yes	Perennial	Europe	Group II
Oenothera rosea	No	Perennial	America	Group III
Opuntia ficus-indica	Yes	Shrub	America	Group III
Opuntia monacantha	Yes	Shrub	America	Group III
Opuntia stricta var.*dillenii*	Yes	Shrub	America	Group III
Oxalis corymbosa	Yes	Perennial	America	Group II
Panicum maximum	Yes	Perennial	Africa	Group I
Panicum repens	Yes	Perennial	America	Group I
Papaver nudicaule	Yes	Perennial	Europe	Group III
Parthenium hysterophorus	No	Annual	America	Group III
Paspalum conjugatum	Yes	Perennial	America	Group I
Paspalum dilatatum	Yes	Perennial	America	Group I
Passiflora foetida	No	Perennial	America	Group III
Peperomia pellucida	Yes	Annual	America	Group II
Pharbitis nil	No	Annual	America	Group III
Phleum pratense	Yes	Perennial	Europe	Group III
Physalis pubescens	No	Perennial	America	Group III
Phytolacca americana	No	Perennial	America	Group II
Pilea microphylla	No	Annual	America	Group III

Table A1. Continued.

Species	Clonality	Life forms	Geographic origins	Invasiveness
Pistia stratiotes	Yes	Annual	America	Group I
Plantago virginica	Yes	Annual	America	Group II
Polymnia uvedalia	No	Perennial	America	Group III
Rhynchelytrum repens	Yes	Perennial	Africa	Group III
Ricinus communis	Yes	Annual	Africa	Group III
Scoparia dulcis	No	Annual	America	Group III
Senecio dubtabilis	Yes	Annual	Europe	Group III
Senecio vulgaris	Yes	Annual	Europe	Group II
Setaria palmifolia	Yes	Perennial	Africa	Group III
Solanum aculeatissimum	No	Annual	America	Group III
Solanum capsicoides	No	Perennial	America	Group II
Solanum erianthum	No	Shrub	America	Group III
Solanum torvum	No	Shrub	America	Group III
Solidago canadensis	Yes	Perennial	America	Group III
Soliva anthemifolia	No	Perennial	America	Group III
Sorghum halepense	Yes	Perennial	Europe	Group I
Spartina alterniflora	Yes	Perennial	America	Group II
Spartina anglica	Yes	Perennial	Europe	Group I
Spergula arvensis	Yes	Annual	Europe	Group I
Spermacoce latifolia	No	Perennial	America	Group III
Stachytarpheta jamaicensis	No	Shrub	America	Group III
Stellaria apetala	No	Perennial	Europe	Group III
Synedrella nodiflora	No	Annual	America	Group III
Tridax procumbens	Yes	Perennial	America	Group II
Trifolum repens	Yes	Perennial	Europe	Group III
Ulex europaeus	No	Shrub	Europe	Group I
Vaccaria segetalis	No	Annual	Europe	Group II
Veronica hederifolia	Yes	Perennial	Europe	Group III
Veronica persica	Yes	Perennial	Asia	Group II
Veronica polita	Yes	Perennial	Asia	Group II
Vetiver zizanioides	Yes	Perennial	Asia	Group II
Waltheria indica	Yes	Perennial	America	Group III
Wedelia chinensis	Yes	Perennial	Africa	Group III
Wedelia trilobata	Yes	Perennial	America	Group I
Xanthium spinosum	No	Annual	America	Group I

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