

THE COMMERCIAL SEED TRADE: AN EARLY DISPERSER OF WEEDS IN THE UNITED STATES¹

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Mack, Richard N. (Department of Botany, Washington State University, Pullman, WA 99164). **THE COMMERCIAL SEED TRADE: AN EARLY DISPERSER OF WEEDS IN THE UNITED STATES.** *Economic Botany* 45(2):257–273. 1991. *Seeds, bulbs, and cuttings of exotic plant species, including plants cultivated exclusively as ornamentals, were being advertised for sale in printed circulars in the United States by 1800. By the end of the 19th century seed trade catalogs were prolific and often listed dozens of exotic species that were already naturalized in the U.S. or new introductions from foreign suppliers. Among the species routinely offered for sale were many now considered noxious (e.g., Berberis vulgaris, Eichhornia crassipes, Isatis tinctoria) or at least undesirable (e.g., Cannabis sativa, Eleusine indica, Lysimachia nummularia). This commerce was not only responsible for the introduction and spread of some species earlier than previously recognized (e.g., Bryonia alba, Schinus terebinthifolius) but also caused the deliberate distribution of other species assumed to have been spread by accident alone (e.g., Aegilops cylindrica, Bromus briziformis, Bromus mollis). Seedsmen's introduction of substantial genetic variation through repeated introductions, inadvertent directional selection for local races in their gardens, their widespread use of seeds (compared to cuttings or non-fertile plant material), and the sowing of seeds at high density under cultivation all enhanced the opportunity for eventual naturalizations. The largely unrecognized proliferation of this industry in the 19th century and the ready access that consumers had to these species via mail order contributed to the rapid and extensive dissemination of at least 139 alien species throughout the United States.*

Der Samenhandel: ein frühen Verbreiter von Unkräutern in den Vereinigten Staaten. *Samen, Zwiebeln, und Stecklinge von exotischen Pflanzenarten, inklusive Pflanzen, die man ausschliesslich als Zierpflanzen kultivierte, wurden schon um 1800 durch Rundschreiben in den USA zum Verkauf angeboten. Zum Ende des 19. Jahrhunderts waren Samenhandelskataloge weitverbreitet und führten oft Dutzende von exotischen Arten, die sich schon in den USA heimisch gemacht hatten, oder neues Material von auslaendischen Lieferanten. Unter den Arten, die ueblicherweise zum Verkauf angeboten wurden, befanden sich nun viele, die heute als schaedlich (z.B. Berberis vulgaris, Eichhornia crassipes, Isatis tinctoria) oder wenigstens als unerwuenscht (z.B. Cannabis sativa, Eleusine indica, Lysimachia nummularia) angesehen werden. Dieser Handel war nicht nur verantwortlich fuer die Einfuehrung und Verbreitung mancher Arten zu einem fruheren Zeitpunkt als bisher vermutet (z.B. Bryonia alba, Schinus terebinthifolius), sondern verursachte ebenso die absichtliche Verbreitung anderer Arten, von denen man annahm, dass sie lediglich durch Zufall verbreitet wurden (z.B. Aegilops cylindrica, Bromus briziformis, Bromus mollis). Der Anstoss zu wesentlicher genetischer Variation durch wiederholte Einfuhr durch Samenhaendler, unbeabsichtigte natuerliche Auslese von lokalen Arten in ihren Gaerten, der weitverbreiteter Gebrauch von Samen (im Gegensatz zu Stecklingen oder anderen Arten der vegetativen Vermehrung), sowie dem dichten Saen von Samen im Anbau, dies alles erhoehete die Gelegenheit zur schliesslicher Naturalisierung. Die weitgehend unerkannte Ausbreitung dieser Industrie im 19. Jahrhundert und der leichte Zugang, den Kunden zu diesen Pflanzenarten per Postversand hatten, trugen zur raschen und ausgedehnten Verbreitung von mindestens 139 fremden Arten in den ganzen USA bei.*

The growth and spread of the alien flora in the United States have long been the subject of intense practical observation (De Schweinitz 1836; Dewey 1897; Forcella and Harvey 1983; Rob-

bins 1940); as early as the 1600's observers were noting the entry and naturalization of plants into North America (Cronon 1983 and references therein). Successive editions of local floras covering approximately the same area are among the best documentation we have of both the tim-

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ing and growth of this alien flora. For instance, Darlington (1918) compared the weed species—which were almost all aliens—in successive floras of Michigan from 1839 to 1915. In less than 100 yr this flora grew from 47 to 147 species, with the fastest rate of introduction in the last quarter of the 19th century. Similarly rapid increases in alien floras can be traced in the successive editions of floras of eastern Washington (Mack 1986) and central Illinois (Myers and Henry 1979).

Such compilations prompt obvious questions dealing first with the circumstances surrounding the introduction of these species into the conterminous U.S. and then the means of their spread within the continental interior. Alien plants have arrived in the U.S. by many agents, ranging from accidental immigrations in ship ballast along coastlines to deliberate introductions by private groups and governmental agencies (e.g., Mack 1986; Ridley 1930; Southern California Acclimatizing Association 1895; Williams 1980). Accidentally introduced plants have spread at radically different rates as packing material, as disseminules attached to animals, and in feces (Dewey 1897; Ridley 1930), and most importantly as contaminants in the seed lots of crops (Mack 1986). The spread of deliberately introduced plants has been equally diverse. Plants in this category have served medicinal or herbal purposes, as forage, and especially as ornamentals. Muenscher (1955) compiled a list of plants that he believed had been introduced for these reasons, and many of these species (e.g., *Artemisia absinthium* L., *Lonicera japonica* Thunb., *Rumex acetosa* L., *Tanacetum vulgare* L.) now commonly appear in regional floras throughout the U.S.

The mode by which these plants and others were deliberately disseminated is often unclear. For instance, was the spread of *Nepeta cataria* L. or *Marrubium vulgare* L., both common medicinal plants of the 19th century, attributable simply to the haphazard transfer of seeds from one person to another? This mechanism acting alone has never seemed an entirely plausible explanation, given the speed with which many alien plants spread throughout the U.S. For example, *Eichhornia crassipes* (Mart.) Solms. had spread to all southeastern states by 1900, even though it was unreported in the U.S. before 1884 (Penfound and Earle 1948). I document here another, largely unrecognized agent that accounts for much of the introduction and spread of many alien

plants once deemed useful but now considered pestiferous—the 19th century commercial seed trade.

THE SEED CATALOGS EXAMINED

The documentation I examined consists of pre-1900 seed catalogs within the extensive Nursery and Seed Trade Catalogs Collection at the National Agricultural Library (NAL) and within the Department of Special Collections at the University of California (Davis). For this paper I examined all pre-1872 catalogs in the NAL collection, plus all catalogs for a selection of years spanning the rest of the 19th century: 1875, 1880, 1883, 1885, 1886, 1888, 1890, 1895, and 1899. Examination of the pre-1900 holdings at UC (Davis) was less systematic. Table 1 represents species listed in at least one catalog that are now naturalized in the U.S.; Tables 2 and 3 compile records for alien species that failed to become naturalized and some prominent native species included in these catalogs, respectively.

Several attributes of these catalogs allow their use as records of alien plant availability and spread. Since merchants revised their catalogs annually, each catalog's year of publication is clearly indicated. Unlike most of their modern counterparts, almost all these pre-1900 catalogs list each species by both scientific and common names. To avoid matching unknown or obscure nomenclature to modern taxon names, I usually tallied only species for which the scientific name has remained unchanged and is listed in Fernald (1950) or another North American flora. Alternative or disputed names are noted in Table 1. I assumed that *Ailanthus glandulosa* = *A. altissima* (Mill.) Swingle, *Pontederia crassipes* = *Eichhornia crassipes*, *Pontederia azurea* = *Eichhornia azurea* (Sw.) Kunth., and *Pueraria thunbergiana* = *P. lobata* (Willd.) Ohwi. I also included in the tally species for which there was an obvious misspelling of a name that has remained unchanged, e.g., *Sorghum halapense* (L.) Pers. [sic].

Interpretations from these records were guided by the following points. Any collection of such archival material is a highly biased record of the past. For example, the majority of the catalogs in the NAL collection are from Massachusetts, New York, and Pennsylvania. While both the earliest and the largest number of 19th century seedsmen likely resided in these states, the Midwest, West and especially the South are certainly

underrepresented in my compilation. Unknown is how many other seedsmen printed catalogs during the 19th century; also unknown is the original source of the plant material and any quantifiable records of the locations to which seeds were mailed. I have avoided drawing conclusions from negative evidence: i.e., the lack or infrequency of a species in these catalogs does not accurately gauge its commercial availability in the 19th century. Most important is my assumption that the seeds, cuttings, etc. were correctly identified.

GROWTH OF THE SEED TRADE INDUSTRY IN THE UNITED STATES: PRE-1865

Circulars and pamphlets advertising seeds, cuttings, bulbs, and tubers were in circulation in the U.S. by at least the last quarter of the 18th century; the oldest record in the NAL is a fruit tree catalog from the William Prince Nursery in Flushing, New York, dated 1771. Not surprisingly, these early catalogs offer primarily a limited selection of crop plants. By 1800 much more extensive catalogs were available in which lists reached several hundred species, including the seeds of ornamental plants and species used in medicine or for seasonings. Among these early 19th century catalogs are the first records of species that are today naturalized in the U.S.: *Amaranthus retroflexus* L. and *Mimosa pudica* L. (catalog of Bernard M'Mahon, Philadelphia, 1804).

John Bartram & Son, early American naturalists, maintained a nursery at Philadelphia from which they advertised in 1807 a much more extensive collection than M'Mahon's. Included among their listing of "trees, shrubs, and herbaceous plants, indigenous to the United States of America. . ." were alien species, including *Lysimachia punctata* L., *Ricinus communis* L., *Rumex acetosella* L., and *Solanum nigrum* L. Correctly listed as alien species were *Artemisia absinthium* L., *Artemisia vulgaris* L., *Rhamnus cathartica* L., *Solanum dulcamara* L., and *Ulex europaeus* L. The Bartram's catalog is intriguing for several reasons. It includes 55 species available at Philadelphia at the beginning of the 19th century that had already or were to become naturalized in the U.S., including *Cannabis sativa* L., *Centaurea cyanus* L., and *Hyoscyamus niger* L. For several of these (*Anthemis cotula* L., *Lamium amplexicaule* L., *Lolium temulentum* L., *Papaver dubium* L., *Tragopogon porrifolius* L.,

Verbascum thapsus L.), the only record that I have found of their sale in the U.S. is Bartram's catalog. Yet, each species has become naturalized in widely separated parts of the U.S.

The diversity of alien species sold after 1820 increased substantially. Bartram's Botanic Garden catalog for 1828 offered a long list of "medicinal and culinary" species, including such aliens as *Arctium lappa* L., *Digitalis purpurea* L., *Euphorbia lathyris* L., *Hesperis matronalis* L., *Isatis tinctoria* L., *M. vulgare*, and *N. cataria*. All these species are now naturalized in the U.S. *Isatis tinctoria*, dyer's woad, is the most serious pest in this group for it is now rapidly spreading in northern Utah and southeastern Idaho (Callihan et al. 1984; Farah et al. 1988). Other now naturalized species sold in the eastern U.S. before 1850 (with the earliest seed catalog record of their sale in parentheses) are *Papaver somniferum* L. (John B. Russell, Boston, 1828), the aggressive *Agrostemma githago* L. (Hovey & Co.'s, Boston, 1845), *Tamarix gallica* L. (W. Prince, Flushing, New York, 1823), the now widespread *Lonicera japonica* (W. Prince, Flushing, New York, 1823), *Cytisus scoparius* (L.) Link (W. Prince, Flushing, New York, 1844-1845), and *Cyperus esculentus* L. (W. Prince, Flushing, New York, 1829).

GROWTH OF THE SEED TRADE INDUSTRY IN THE UNITED STATES: POST-1865

Any chronological division of the 19th century seed trade is necessarily subjective, but I have chosen to divide these records with the end of the American Civil War. After 1865 the volume and extent of rail traffic and consequently the size of seedsmen's potential markets increased markedly (U.S. Bureau of the Census 1895). Information in seed catalogs supports the use of the mid-1860's as an appropriate time line. Catalogs in circulation in the late 18th and the first half of the 19th century suggest that markets were small: seeds, etc. could be shipped but, more commonly, instructions in the catalogs indicate that customers made their purchases at the seed house or nursery. Potential markets expanded as postal rates for printed matter repeatedly fell between 1845 and 1852 (Roper 1917). Not only could circulars be inexpensively mailed hundreds of miles, but the orders could also be filled by mail or rail freight. By 1875 seedsmen routinely enclosed order forms in their catalogs, and

most sales for the larger businesses would have occurred by mail. Soon many seedsmen were clearly catering to a regional or even national market. For example, seedsmen in New York, La Crosse, Wisconsin and Philadelphia sold *Atriplex semibaccata* R. Br., a native of Australia, with statements in their advertising that this species did well in arid western environments. The inclusion of species in these catalogs for markets hundreds or even thousands of miles away is also seen for other species, including *Eucalyptus globulus* Labill. (catalog of D. M. Ferry & Co., Detroit, Michigan, 1880) and *Grevillea robusta* A. Cunn. (catalog of Alfred Bridgeman, New York, 1899). One indirect gauge of the size of these markets is provided by the testimonials of satisfied customers. It is common to find a seedsman from, say, Georgia, reprinting correspondence received from throughout the eastern third of the U.S., or even the U.K. Well before 1900 some American seedsmen had become international as well as national traffickers in living plant material.

This trade had, of course, long operated in both directions across the Atlantic, and the European seed trade had a sustained influence on the seed trade industry in the U.S. and the species sold. Most of the new ornamental varieties in each year's catalogs were clearly indicated as imports from Europe. Many British and German firms sold thousands of species through catalogs. For instance, the 1868 catalog of Haage & Schmidt (Erfurt, Germany) listed 12,471 taxa, including such unlikely commercial species as *Bromus tectorum* L. By importing plants from European firms, U.S. seedsmen were drawing on immense collections. As a result, some seedsmen began producing catalogs that were several hundred pages long; a few annually produced half a dozen catalogs, each specializing in one part of the burgeoning seed trade (e.g., Peter Henderson & Co's., New York, 1890). By 1899 hundreds of firms operated in the northeastern U.S. alone, many annually producing catalogs adorned with elaborate multi-colored prints of the plants they sold (see Mack 1990).

THE DIVERSITY OF WEEDY ALIEN SPECIES SOLD BY 1900

Of the hundreds of alien species sold in the 19th century, comparatively few have become naturalized in the U.S. Table 1 tallies those 139 naturalized taxa sold from 1804 to 1899 for which

the species' names have remained unchanged. Many species within this list, such as *Briza maxima* L. and *Marrubium vulgare*, present little or no environmental threat. Others (e.g., *Lysimachia punctata*, *Tanacetum vulgare*) are frequently nuisances and locally persistent but not particularly aggressive. The remaining list comprises some of the worst weeds found in the U.S. today (e.g., *Berberis vulgaris* L., *Eichhornia crassipes*, *Sorghum halepense*), including one species on the Federal Noxious Weed List, *Eichhornia azurea* (Westbrooks 1981). As a group they illustrate the diversity of ornamental, forage, and medicinal plants available before 1900.

The importation and sale of alien graminoids for forage has been practiced in the U.S. for at least 3 centuries: Cronon (1983) reported that a routine commerce was established in southern New England by the 1640's in the seeds of "English grasses"—probably species such as *Poa pratensis* L. My concern here is with a sedge and a grass that were first sold for forage production. Some of the worst weeds are sedges in the genus *Cyperus* (Holm et al. 1977). *Cyperus esculentus*, yellow nut-grass, is a perennial tuber-bearing sedge native to the Old World (Godfrey and Wooten 1979). In addition to being a serious pest in tropical Africa, the species includes ecotypes that infest crops in the southeastern U.S. (Holm et al. 1977). Seedsmen may have played only a minor role in the spread of yellow nut-grass in the U.S.; I found only one supplier who sold *Cyperus esculentus* (W. Prince, Flushing, New York), and this firm sold it for only about a decade before 1840. But even a short commercial history may have been sufficient to establish the foci for the sedge's later spread.

Sorghum halepense (Johnson grass), one of the most troublesome alien plants in the U.S., has a much more extensive commercial history. This perennial grass displays both high fecundity and vigorous vegetative growth. In addition, it is an aggressive competitor and difficult to eradicate (Holm et al. 1977). More serious is its ability to introgress with commercial sorghum thereby producing commercially useless offspring called shattercane (Baker 1972). Johnson grass is one of the few wild species that might produce offspring more "weedy" than itself through hybridization with a domesticated transgenic relative (NAS 1989). McWhorter (1971) argued that *S. halepense* was probably in the U.S. by 1830. He pointed out that its early history in North Amer-

Table 1 (Continued)

Catalog Date	Seedsman Location	Catalog Date	Seedsman Location
<i>C. moschata</i> (Continued)			
1852	NY	1883	NY
1854	MA	1885	NY
1862	PA	1890	NY
1863	PA; NY		
1866	NY		
1869	NY (3); PA		
1870	NY		
1889	PA*		
1894	PA*		
<i>Centaurea nigra</i> L.			
1833	MA		
1841	NY		
1844/45	NY		
1845/46	NY		
<i>Cerastium tomentosum</i> L.			
1870	NY		
<i>Chenopodium botrys</i> L. ^d			
1807	PA		
1827	NY		
1834/35	MA		
1843	DC		
<i>Conium maculatum</i> L.			
1807	PA		
1825	NY		
1826	NY		
1828	NY		
1829	NY		
1831	NY		
1874	NJ*		
1875	NY*; NY (2)		

Table 1 (Continued)

Catalog Date	Seedsman Location	Catalog Date	Seedsman Location
<i>Digitalis purpurea</i> L.			
1807	PA		
1811	PA		
1825	NY		
1826	NY; PA		
1827	NY		
1828	PA		
1829	NY		
1833	MA		
1834/35	MA		
1835	MA; OH		
1838	MA		
1840	MA		
1841	NY		
1842	MA		
1843	DC		
1844/45	PA		
1845	MA		
1845/46	NY		
1846	MA		
1846/47	OH		
1847	NY		
1848	OH		
1852	NY		
1853	NY		
1854	MA		
1859	MA; RI*		
1860	MA		
1862/63	NB		
1863	NY		
1866	MA		
1867	MA		
1869	MA (2); NY (2)		
1870	MA; NY		
1875	NY (3)		
1877	NY*		
1880	MA (2); NY (2); PA		
1883	IL*; NY*		
1885	MA; NY		
1888	NY		
1889/90	NY		
1890	MA; NY; PA		

Catalog Date	Seedsman Location	Catalog Date	Seedsman Location
<i>C. dactylon</i> (Continued)			
1899	CA (2); OH; OR; WA		
<i>Cyperus esculentus</i> L.			
1829	NY		
1831	NY		
1839	NY		
<i>Cytisus scoparius</i> (L.) Link			
1844/45	NY		
1845	NY (2)		
1846/47	NY; OH		
1847	NY		
1848	OH		
1852	NY (2)		
1861	NJ		
1863	NY		
1869	NY		
1871/72	CA*		
1885	MD		
<i>Dacrydium glomerata</i> L.			
1826	MD		
1835	OH		
1845	MA		
1870	NY		
1875	NY*		
	NY (2); NY*		
1877	NY*		
1885	NY		
1888	LA; PA (2)		
1890	LA; LA; MA; NY (2); PA (3)		

Catalog Date	Seedsman Location	Catalog Date	Seedsman Location
<i>Dipsacus sylvestris</i> Huds. ^m			
1825	NY		
1826	NY		
1828	PA		
1829	NY		
1831	NY		
<i>Echinochloa colonum</i> (L.) Link			
1870	NY		
1871	NY		
1875	NY		
1880	NY		
1883	NY		
<i>Echinops spheerocephalus</i> L.			
1807	PA		
1826	PA		
1835	MA		
1836	MA		
1852	NY		
<i>Echium plantagineum</i> L. ^d			
1847	NY		
1899	MA; PA		
<i>Eichhornia azurea</i> (Sw.) Kunth. ⁿ			
1884/85	NJ		
1890	PA		
1892	FL*		
1893	FL*		
1895	NJ		
1899	PA		

Table 1 (Continued)

Catalog Date	Seedsman Location	Catalog Date	Seedsman Location
<i>Eucalyptus globulus</i> Labill. ^d			
1871/72	CA*		
1874	CA* (2)		
1875	NY		
1875/76	FL*		
1880	MI*		
1882	CA*		
1883	MA		
1884	CA*		
1886	CA*		
1890	CA* (2); NY; PA		
1894/95	CA*		
1895	NY*		
1898/99	CA		
1899	CA (4); OR; WA		
<i>Eucalyptus polyanthemus</i> Schauerr. ^d			
1898/99	CA		
<i>Eucalyptus verticornis</i> Sm. ^d			
1898/99	CA		
1899	CA		
<i>Euphorbia cyparissias</i> L.			
1833	MA		
1841	NY		
1844/45	NY		
<i>Euphorbia laevis</i> L. ^d			
1807	PA		
1825	NY		
1826	NY		

Table 1 (Continued)

Catalog Date	Seedsman Location	Catalog Date	Seedsman Location
<i>E. laevis</i> (Continued)			
1842	MA		
1844/45	NY		
1845	MA		
1845/46	NY (2)		
1846	MA		
1846/47	OH		
1847	NY (2)		
1852	NY		
1854	MA		
1859	MA		
1860	MA		
1862	MA		
1868	PA		
1869	MA; NY; PA		
1895	MI*		
<i>Hieracium aurantiacum</i> L.			
1875	NY		
1880	NY		
<i>Hyoscyamus niger</i> L.			
1807	PA		
1825	NY		
1826	NY; PA		
1827	NY		
1828	PA		
1829	NY		
1833	MA		
1834/35	MA		
1841	NY		
1843	DC		
1846	MA		
1852	NY		
1875	NY		
1890	IA; NY		
1895	MI		
<i>Indula helenium</i> L.			
1807	PA		
1811	PA		
1825	NY		
1826	NY; PA		
1827	NY		
1828	NY; PA		
1827	DC; NY		
1828	PA		
1829	NY		
1833	MA		
1834/35	MA		

C. maculatum (Continued)

Convovulus arvensis L.^b

Convovulus sepium L.^{d1}

Crotalaria retusa L.

Cynara cardunculus L.^d

Cynodon dactylon (L.) Pers.

Dactylis glomerata L.

Eichhornia crassipes (Mart.) Solms.^a

Eleusine indica (L.) Gaertn.

Elymus caput-medusae L.^{dn}

Erodium cicutarium (L.) L'Her.

Grevillea robusta A. Cunn.^f

Hedychium gardenianum Roscoe^g

Hesperis matronalis L.

H. laevis (Continued)

Hypericum perforatum L.

Hystosopus officinalis L.

Ipomoea coccinea L.

I. helenium (Continued)

Table 1 (Continued)

Catalog Date	Seedsman Location	Catalog Date	Seedsman Location	Catalog Date	Seedsman Location
<i>Ipomoea quamoclit</i> L.		<i>Kochia scoparia</i> (L.) Roth		<i>Lonicera japonica</i> Thunb.	
1804 PA		1847 NY		1823 NY	
1807 PA		1852 NY		1825 NY	
1810 MD		1856 NY		1826 PA	
1834/35 MA		1886 NY		1828 PA	
1835 OH		1890 NY		1832 NY	
1838 MA				1844/45 PA	
1840 MA		<i>Lamium amplexicaule</i> L.		1845 PA	
1842 MA				1845/46 NY	
1845 MA		1807 PA		1846/47 NY; OH	
1847 NY (2)				1847 NY	
1852 NY				1848/49 NY	
1853 NY				1849 PA	
1854 MA		<i>Lantana camara</i> L. ^c		1850/51 MA	
1859 MA				1852 NY	
1862 NY		1804 PA		1855 MA	
1863 NY; PA		1826 PA		1858 GA	
1866 MA		1828 PA		1861 GA	
1869 NY; PA (3)		1830 NY		1871 MO; PA	
1870 NY (3)		1852/53 NY		1874 CA*	
1875 NY (3)		1858 IL		1875 NY	
1880 LA; MA (2); ME (2); NY (4)		1862 NY		1875/76 FL*	
1883 MA		<i>Lespedeza striata</i> (Thunb.) H. & A.		1880 NY	
1885 MA; NY (2)				1889/90 FL*	
1888 PA		1888 LA		1890 NY (2)	
1890 FL; MA; NY (3)		1890 LA; NY (2); PA (2)		<i>Lychnis alba</i> Mill. ^o	
				1831 NY	
<i>Isatis tinctoria</i> L.		<i>Linaria dalmaica</i> (L.) Mill.		1839 NY	
1807 PA				1843 NY	
1825 NY (2)		1899 CO		1847 NY	
1826 MD; NY				1852 NY	
1827 NY				1859 MA	
1828 MA; PA		<i>Lolium temulentum</i> L.		1862 MA; NY;	
1829 NY				1863 NY	
1831 NY		1807 PA		1866 MA	
1833 MA				1868 PA	
1834/35 MA				1869 MA (2); NY	
1843 DC				1870 MA; NY	
1847 NY				1876 NY*	

Table 1 (Continued)

Catalog Date	Seedsman Location	Catalog Date	Seedsman Location	Catalog Date	Seedsman Location
<i>L. alba</i> (Continued)		<i>Lychnis dioica</i> L. ^P		<i>Lysinachia punctata</i> L.	
1877 NY*		1807 PA		1807 PA	
1880 NY		1829 NY		1888 MA*	
1885 NY		1831 NY			
1888 MA*; MA		1839 NY		<i>Lythrum salicaria</i> L.	
1890 MA; NY; PA				1829 NY	
1895 NY*		<i>Lychnis flos-cuculi</i> L.		1831 NY	
1899 MA				1833 MA	
		1831 NY		1835 OH	
<i>Lychnis chalconica</i> L.		1833 MA (2)		1841 NY	
1807 PA		1835/36 NY		1844/45 NY (2)	
1811 PA		1839 NY		1845/46 NY	
1824 PA		1841 NY		1846 MA	
1826 NY; PA		1844/45 NY (2)		1846 MA	
1827 NY		1845/46 NY		1846/47 OH	
1828 PA		1846 MA		1848 OH	
1831 NY		1846/47 OH		1848 OH	
1833 MA		1848 OH		1853 ME	
1841 NY		1848 OH		1869 NY	
1843 NY		1853 ME			
1844/45 NY (2); PA				<i>Marrubium vulgare</i> L.	
1845 OH				1807 PA	
1845/46 NY		<i>Lysinachia nummularia</i> L.		1825 NY	
1846 MA				1826 NY; PA	
1846/47 OH		1833 MA		1827 DC	
1847 NY		1841 MA		1828 NY	
1848 OH		1843 NY		1828 MA; PA	
1852 NY		1844/45 NY		1829 NY	
1853 ME		1854 MA		1833 MA	
1854 MA		1859 MA		1834/35 MA	
1859 MA		1869 NY		1841 NY	
1860 MA		1870 OH		1843 DC	
1862 MA; NY; PA		1874 NY*		1845 NY	
1863 NY; PA		1875 NY; OH; RI*		1846 MA	
1866 MA; NY		1880 NJ; NY		1847 NY	
1867 MA		1885 MA		1848 MA	
1868 PA		1886 NY		1849 NY	
1869 MA (2); NY (5); PA		1888 DC; KY; MA		1850 NY*	
1870 MA; NY (2); OH		1890 NJ; NY		1852 NY	
		1891 NJ*		1854 MA	
		1893 NJ		1855 NY*	
		1899 WI		1856 NY	
				1857 NY	
				1858 MI*	
				1859 MI*	
				1860 NY; PA	
				1861 NY	
				1862 NY	
				1863 NY; PA	
				1864 DC	
				1865 NY	
				1866 NY	
				1867 NY	
				1868 NY*	
				1869 NY	
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				1987 NY	
				1988 NY	
				1989 NY	
				1990 NY	
				1991 NY	

Table 1 (Continued)

Catalog Date	Seedsman Location	Catalog Date	Seedsman Location	Catalog Date	Seedsman Location
<i>Medicago lupulina</i> L.		<i>Mesembryanthemum crystallinum</i> L. ^d		<i>M. pudica</i> (Continued)	
1807 PA				1871 MI*; NY	
1826 MD		1807 PA		1875 NY	
1834/35 MA		1811 PA		1880 MA	
1847 NY		1824 PA		1885 MA; NY (2)	
1852 NY		1826 PA		1886 PA	
1875 NY		1827 NY		1887/88 FL	
1886 PA		1828 PA		1888 LA; NY (2); OH; PA	
1888 PA		1834/35 MA		1890 NY	
1890 NY (2)		1835 OH		1899 MA; NY*	
		1838 MA			
		1840 MA		<i>Myrica faya</i> Ait. ^f	
		1842 MA			
		1845 MA		1825 NY	
		1847 NY (2)		1826 PA	
		1851 MA		1830 NY	
		1852 NY		1832 NY	
		1859 MA			
		1860 MA		<i>Nepeta cataria</i> L.	
		1862 MA			
		1863 NY		1807 PA	
		1866 MA; NY		1825 NY (2)	
		1867 MA		1826 NY	
		1868 PA		1827 DC; NY	
		1869 MA (3); NY (2); OH		1828 MA; PA	
		1870 NY (2); OH		1834/35 MA	

Table 1 (Continued)

Catalog Date	Seedsman Location	Catalog Date	Seedsman Location	Catalog Date	Seedsman Location
Ranunculus acris L.					
1826	NY	R. communis (Continued)			
1829	NY	1870	NY (2); OH	R. graveolens (Continued)	
1831	NY	1874	NJ*	1829	NY
1841	NY	1875	NY*	1841	NY
1844/45	NY		NY (2)	1843	DC
1845/46	NY (2)	1876	NY*	1846	MA
1846	MA	1880	MA; ME;	1852	NY
			NY (3)	1875	NY
		1883	IL; NY	1895	MI*
		1884	NY*	Saponaria officinalis L.	
		1885	MA; NY	1807	PA
		1887/88	FL	1811	PA
		1890	FL; MA; NY	1826	NY; PA
				1829	NY
		Rosa multiflora Thunb.			
1807	PA	1826	PA	1831	NY
1826	NY; PA	1828	PA	1833	MA
1828	PA	1849	PA	1839	NY
1829	NY	1852	NY	1841	NY
1831	NY	1849	NY; PA	1844/45	NY; PA
1833	MA	1852	NY	1859	MA; RI*
1841	NY	1889/90	NY	Tussilago farfara L.	
1843	NY	Rumex acetosella L.			
1844/45	NY (2)	1807	PA	1807	PA
1845	NY	Rumex crispus L.			
1845/46	NY	1807	PA	1823	NY
1846/47	NY; OH	1888	MA	1825	NY
1850/51	MA	Rumex obtusifolius L.			
1855	MA	1807	PA	1827	DC
1869	MA	Ruta graveolens L.			
1875	NY (2)	1807	PA	1829	NY
1882	CA*	1825	NY	1841	NY (2)
1883	NY	1827	DC; NY	Ulex europaeus L.	
1884	CA*	Schinus molle L.^d			
1885	MA; MD	1832	NY	1807	PA
1888	MA; NY	1838	PA	1823	NY
1890	MA; NY (3); PA (2)	1844/45	PA	1825	NY
1899	IN; NY (3)	1868	IL	1827	DC
Ricinus communis L.					
1807	PA	1869	MA	1829	NY
1834/35	MA	1874	CA*	1831	NY
1843	DC	1880	MA	1832	NY
1852	NY	1882	CA*	1833	MA
1866	MA	1890	CA; NY	1841	NY
		1899	CA; NY	1843	NY
		Schinus terebinthifolius Raddi^e			
		1832	NY	1844/45	PA
		1899	CA	1845/46	NY
				1846/47	NY
				1847	NJ; NY

Table 1 (Continued)

Catalog Date	Seedsman Location	Catalog Date	Seedsman Location	Catalog Date	Seedsman Location
Solanum dulcamara L.					
1807	PA	Spergularia arvensis L.			
1826	PA	1885	NY	T. gallica (Continued)	
1828	PA	1890	NY	1844/45	NY
1829	NY	1894/95	CA*	1845	NY (2); PA
1833	MA	1895	MI*	1845/46	NY (2)
1841	NY	1899	CA; IL (2); MA; MI;	1847	NJ
1844/45	NY		NY (2)	1848	NJ
1845	NY	Tamarix africana Poir.^e			
Solanum nigrum L.					
1807	PA	1852	NJ; NY	1848/49	NY
Sorghum halepense (L.) Pers.					
1883	LA	1858	VA	1849	PA
1883	IL; NY	1859	RI*	1850/51	MA
1885	MI*; NY	1869	NY	1852	NJ; NY
1886	LA; NY (3); PA (2)	1875	NY	1856	CA*; NY
1888	LA; MI; NY; PA (2)	1877/72	CA*	1859	NY
1890	CA; LA; MI*; NY (2); OR; PA (2)	1886	MA	1869	NY
1894/95	CA*	1888	MA	1871	NY
1895	GA; MI*	1889/90	NY	1888	MA
1899	CA (4); GA; LA; MO (2); NB; NY (5); OH; OR (2); PA (2); VA; WA (2); WI (2);	1890	NY (2)	1889	NY
		1899	NJ; NY (2)	Tamarix tetrandra Pall.^d	
				1875	NY
				1888	NY; PA
				1890	NY
				1899	NJ
		Tanacetum vulgare L.			
		1823	NY	1807	PA
		1826	NY	1825	NY (2)
		1828	PA	1827	DC
		1829	NY	1827	NY
		1831	NY	1828	MA
		1833	MA (2)	1829	NY
		1841	NY	1833	MA
		1841	NY	1841	NY
		1843	NY	1852	NY
				1874	NI*
				1875	NY*; NY (2)
				1880	PA

Table 1 (Continued)

Catalog Date	Seedsman Location	Catalog Date	Seedsman Location
T. vulgare (Continued)			
1885	MA; MI*;	Ulex europaeus L.	
	NY	1848	NJ
1890	MI*; NY (2)	1852	NY
1895	MI*; NI*	1885	MD
1899	MI*	1890	NY; PA
		1894/95	CA*
		1899	CA; NY
Taraxacum officinale Weber			
1895	MI*	Verbascum thapsus L.	
		1807	PA
Tragopogon porrifolius L.			
1807	PA	Xanthium strumarium L.	
		1807	PA
* Correll and Johnston (1970)			
b Hitchcock <i>et al.</i> (1959)			
c Long and Lakela (1971)			
d Munz (1959)			
e Munz (1974)			
f Neal (1965)			
g Roche and Talbot (1986)			
h Welch <i>et al.</i> (1987)			
i equals <i>Chamaemelum nobile</i> (L.) Aill. (Tutin <i>et al.</i> 1976)			
j equals <i>Galium odoratum</i> (L.) Scop. (Tutin <i>et al.</i> 1976)			
k equals <i>Bromus hordeaceus</i> L. subsp. <i>hordeaceus</i> (Tutin <i>et al.</i> 1980)			
l equals <i>Calyptegia sepium</i> (L.) R. Br. (Tutin <i>et al.</i> 1972)			
m equals <i>Dipsacus fullonum</i> L. (Tutin <i>et al.</i> 1976)			
n equals <i>Taeniatherum capus-medusae</i> (L.) Nevski (Tutin <i>et al.</i> 1980)			
o equals <i>Silene latifolia</i> Poir. subsp. <i>alba</i> (Mill.) Greuter & Burdet (Clapham <i>et al.</i> 1987)			
p equals <i>Silene dioica</i> (L.) Clairv. (Clapham <i>et al.</i> 1987)			
q equals <i>Malva pusilla</i> Sm. (Tutin <i>et al.</i> 1968)			

ica is clouded by the number of common and scientific names under which it has been known. Consequently, its seeds may have been sold early in the 19th century under various pseudonyms, but the earliest reference that I have seen to “*Sorghum halepense*” in seed catalogs appeared in 1883 (catalog of R. Frotscher, New Orleans). It was commonly sold for the remainder of the century throughout the U.S. (Table 1). Even while being touted as a productive forage grass, some seedsman (e.g., catalog of R. Frotscher, New Orleans, 1886) were cautioning their customers not to sow Johnson grass near cultivated fields, as “It is almost impossible to get it out of land.” One seed firm, Johnson & Musser of Los Angeles, California, stated in its 1899 catalog that, “It is so difficult to eradicate from soil when once established that we do not recommend it,” but they nevertheless sold the grass.

Grasses were also widely sold in the late 19th century for use in “immortelles,” i.e., dried flower arrangements and wreaths. While the use of dried grasses as ornamentals is common today, the choice of species that filled Victorian vases often proved unwise. *Aegilops cylindrica* L., jointed goat grass, was among the worst. This

grass is a serious weed in cereal fields in the central Great Plains and the Pacific Northwest (Donald 1980; Swan 1984) because it is related to wheat, thus complicating the use of some herbicides. Furthermore, there remains the unresolved possibility that *A. cylindrica* can hybridize with wheat to produce fertile hybrids (Swan 1984). So far, the danger from such introgression however appears small (A. Ogg, personal communication). Another ornamental grass of that era, *Eleusine indica* (L.) Gaertn. (goose grass) is a major pest worldwide (Holm et al. 1977). In southeastern U.S. it commonly infests fields of cotton, peanuts, and sorghum (Elmore 1984). The dried inflorescences of at least five alien annual bromes (*Bromus briziformis* Fisher. & Mey., *B. madritensis* L., *B. mollis* L., *B. secalinus* L., and *B. sterilis* L.) were also considered of ornamental value. All of these bromes are common weeds of cereal fields, and they may be locally prominent. *Bromus mollis* is a prevalent alien brome in the Central Valley of California, and *B. secalinus* and *B. sterilis* are widespread in the U.S. (Muenscher 1955). Other weedy alien grasses sold as ornamentals include *Elymus caput-medusae* L. and *Briza minor* L. The marketing of these grasses illustrates that some alien plants owe their spread to purposes for which they have long since been discarded. It would be difficult if not impossible today to detect the impetus for their original dissemination were their early use not so clearly indicated in 19th century seed catalogs.

The largest single group in Table 1 is herbaceous dicots. Most were distributed as ornamentals; the rest were used for medicine or seasonings. No one species completely characterizes this diverse group, although the historical use and spread of *Centaurea cyanus* (cornflower, bachelor's button) is instructive. This annual composite was available commercially by at least 1807. According to Bailey (1914), it became one of the most popular garden plants in the U.S., probably because of its variably colored corollas (blue, purple, pink, or white), plus its ability to flower until frost. Another trait that Bailey noted—the ability to set seed in autumn and emerge in the spring with little or no cultivation—has contributed to its role as a weed. This ability and a wide ecological amplitude have allowed cornflower to become one of the most widely distributed alien plants in the U.S.; it is commonly found along roadsides, agricultural fields, and other sites of continual disturbance (Fernald 1950; Hitchcock

et al. 1955; Munz 1959; Radford et al. 1968; Steyermark 1963). Unlike most other species in Table 1, cornflower is still available commercially.

Medicinal plants were sold throughout the 19th century, although they were probably most common in pre-1865 catalogs; plants such as *Papaver somniferum* (opium poppy) and *Cannabis sativa* (hemp) were included. To the 19th century seedsman and his customers, *C. sativa*, was a multi-purpose plant for which different varieties were sold; one variety for hemp or fiber production; another variety for the production of oil (seeds). These varieties (and others designated in the 19th century) do not deserve separate taxonomic status, as these products can be produced from any *C. sativa* (Schultes 1970). Haney and Bazzaz (1970) maintained that naturalized *C. sativa* resulted from plants cultivated for fiber or oil; naturalizations could have also resulted from uneaten bird seed, another common use for which hemp seeds were widely sold at that time (catalogs of R. H. Allen & Co., New York, 1870 and B. K. Bliss & Sons, New York, 1883). There is no evidence in U.S. seed catalogs that hemp was sold in the 19th century to produce its well-known cannabinoids. As Schultes (1970) proposed, the explanation may lie in the widespread belief at that time that only hemp grown in India produced pharmaceuticals.

Some of the most damaging and persistent weeds are aquatic vascular plants (Holm et al. 1969). In addition to competing with native submerged plants for light, they may grow so vigorously as to block navigable waterways and may even provide habitat for the insect vectors of malaria and encephalomyelitis (Holm et al. 1977; Vietmeyer 1975). Unfortunately, some of the worst aquatic plants were sold as ornamentals in the U.S. in the 19th century, including both *Eichhornia azurea* and *E. crassipes* and almost certainly *Myriophyllum brasiliense* Camb. (termed *M. proserpinacoides* in most 19th century catalogs).

Information provided by seed catalogs on the introduction of *Eichhornia crassipes* (water-hyacinth) into the U.S. is particularly revealing. Heretofore the accepted account of water-hyacinth's entry begins with its display at the Cotton Centennial Exhibition in New Orleans in 1884. This attractive aquatic plant was handed out at the exhibition and presumably the attendees dispersed the plant locally—an account ap-

parently first given by Klorer (1909) and reiterated since then (Barrett 1989; Penfound and Earle 1948; Sculthorpe 1967). But water-hyacinth was available as *Pontederia crassipes* by at least 1884 from the catalog of Edmund D. Sturtevant of Bordentown, New Jersey. Furthermore, the plant was available from the German firm Haage & Schmidt repeatedly in the 20 yr preceding the Cotton Exhibition. How much these two early sources may have contributed to its spread in the U.S. is unknown. But the plant soon attracted the attention of many other U.S. nurserymen: by 1888 it was being sold by Henry A. Dreer in Philadelphia, one of America's largest seed houses. By 1895 it was being extolled with much purple prose by seedsmen as widely separated as New York, Florida, and California (Table 1).

Given the environmental damage water-hyacinth was soon to wreak on the lower Mississippi drainage and elsewhere (Sculthorpe 1967), the advice in some of these catalogs to grow the plant outdoors in pools is chilling (catalog of John L. Childs, Floral Park, New York, 1895). As with *Sorghum halepense*, apocalyptic statements were sometimes voiced about the dangers of disseminating the plant, but the advice was already too late. For example, the Royal Palm Nurseries (Oneco, Florida) matter-of-factly stated in its advertisement for water-hyacinth for 1899 that it, "Has proved to be a nuisance in Florida rivers and lakes, forming large masses and obstructing navigation." That assessment was an understatement; by 1897 water-hyacinth was becoming a major navigation hazard on several rivers in Florida (Webber 1897), compelling Congress to provide funds to combat it (U.S. Congress. House. 55th Cong., 3rd sess., 1899, H. Doc. 91). Consequently, the 19th century closed with an expanding list of merchants actively selling water-hyacinth, while the federal government was actively seeking its control.

With the exception of edible gourds and grapes, viney species were sold principally as ornamentals in the 19th century (e.g., *Hedera helix* L., *Wisteria sinensis* Sweet). Most of these ornamental vines have not become weedy in the U.S., although two vines have become naturalized pests (Table 1). Unlike many of the other cucurbits sold in the latter half of the 19th century, *Bryonia alba* L. produces neither an edible nor a showy pepo [cf. *Echinocystis lobata* (Michx.) T. & G.]. Preparations from *Bryonia* fruits have been used since antiquity as emetics and cathartics in

southern Europe (Hamilton 1852), although the plant appears to have been sold in the U.S. only for its ornamental value. Despite repeated sales in the 19th century, this perennial vine apparently failed to become naturalized in most of the U.S. However, in the last 25 yr or more it has spread in southeastern Idaho, Montana, northern Utah, and especially southeastern Washington (Dorn 1984; R. N. Mack, personal observations; Welch et al. 1987). I do not know whether these current invasions of *B. alba* stem from introductions made long ago by commercial seedsmen, although it may not be coincidental that at one site in Cache Co., Utah, *B. alba* was found in a long-abandoned garden with other ornamental cucurbits (R. Alan Black, personal communication).

In autumn 1876 the U.S. Centennial Commission took the farsighted action of appointing a committee to inspect the Philadelphia site of the recently concluded international exhibition for insects and plants that had been introduced as a result of the foreign exhibits. The committee was diligent to a fault; they delayed reporting until 5 yr later, "in the belief that some solitary plants might be overlooked, which producing seed and increasing in following seasons, might then be discovered by their greater numbers" (LeConte et al. 1881). Despite their diligence, the five person committee could not have known at the time that a deliberate plant introduction would become the most serious pest resulting from the Exhibition, kudzu (*Pueraria lobata*). According to the catalog of the Jessamine Gardens (Florida) for 1899, the plant was introduced at the Exhibition's Japanese exposition. Kudzu may have entered the commercial nursery market soon thereafter as several nurseries in the early 1880's offered vaguely described vines that might have been kudzu. The earliest reliable catalog record I have seen of its sale in the U.S. is by H. H. Berger (San Francisco) in 1895. Whether this supplier had acquired stock from the original 1876 introduction is unresolvable. But by the last decade of the 19th century additional material was being exported directly from Japan by several nurseries (F. Takaghi, Tokyo, 1894, 1897, 1898; Yokohama Nursery Co. Ltd, Yokohama, 1898). Consequently, the last decade of the 19th century saw entries of kudzu into the U.S. from Japan that all pre-date introductions of the vine by the U.S.D.A. (cf. Anonymous 1905).

Certainly the worst woody plant widely sold by 19th century seedsmen is *Berberis vulgaris*, the intermediate host of the wheat rust fungus *Puccinia graminis*. This European shrub was being sold in the U.S. by at least 1841, and it was commonly sold in the northeastern U.S. by 1899. Given its availability in the 19th century, it is not surprising that its eradication during World War I would require a massive effort employing thousands of workers and even school children (Hutton 1928). Other introduced shrubs, while less pestiferous than *B. vulgaris*, have nevertheless become invasive. *Rhamnus cathartica*, the English buckthorn, is locally a serious weed in the Midwest (Leitner 1985). *Cytisus scoparius*, Scotch broom, and *Ulex europaeus*, gorse, were sold early in the 19th century; for instance, gorse was sold at the Bartram's garden by 1807. Although the popularity of Scotch broom seems to have waned after the American Civil War, gorse was still sold in 1899. The history of dissemination of Japanese honeysuckle, *Lonicera japonica*, is confused because *Loniceras* were sold under varietal names much earlier in the 19th century than most other woody ornamentals. Listings in Table 1 are restricted to only those records specifically designated as "*Lonicera japonica*." But the number of vendors selling the shrub under myriad varietal names was likely much larger.

Few alien trees have become serious weeds in the U.S., although most of these species were sold by 19th century seedsmen and nurserymen. Apparently tamarisks, such as *Tamarix africana* Poir. and *T. gallica* were popular lawn trees even before 1865 (e.g., catalogs of William Prince, Flushing, New York, 1823 and Thomas Hancock, Burlington, New Jersey, 1852). Tamarisks sold under one or more names have become serious plant invaders along waterways, especially in the American Southwest (Christensen 1962; Robinson 1965). As a group these species reputedly act as phreatophytes and may detrimentally alter salt concentrations on the soil surface (Hem 1967; van Hylckama 1974).

Most 19th century seedsmen and nurserymen resided in the northeastern quarter of the country, yet they actively sold several semi-tropical or tropical trees that became serious weeds in the southern U.S. and Hawaii, including *Casuarina equisetifolia* Forst., *Psidium cattleyanum* Sabine, and *Schinus terebinthifolius* Raddi. *Schinus terebinthifolius*, Brazilian-pepper, was sold as an

ornamental tree. With its bright red fruits and waxy leaves it has gained wide acceptance in Hawaii and Florida as a Christmastide substitute for holly (Morton 1978). Morton (1978) surmised that Brazilian-pepper was first introduced into the U.S. at the turn of this century by the Plant Introduction Service. But this tree was sold over 60 yr earlier in New York (Table 1), and it seems unlikely that even the seeds advertised in the Park Nursery catalog (Pasadena, California) for 1899 were derived from the Plant Introduction Service. Brazilian-pepper possesses features that have facilitated its spread, ensured its persistence, and prompted the concern for its control. Its fruits are commonly spread by frugivorous birds; in the Everglades birds carry the invader to remote hammocks from which it is difficult to remove. As a result, it may now be the most serious plant invader in the Everglades (Toops 1979). In addition, its stems and fruits produce a variety of compounds that cause respiratory problems and contact dermatitis in humans (Morton 1978). *Psidium cattleyanum* (strawberry guava), along with *S. terebinthifolius*, was sold as early as 1832 as both an ornamental and for fruit production. *Casuarina equisetifolia* was also sold beginning early in the 19th century for the shade provided by its unusual foliage of minute, whorled leaves.

SPECIES THAT HAVE FAILED TO BECOME NATURALIZED

Although my emphasis has been on exotic species that became naturalized through their sale in seed catalogs, many other species were repeatedly introduced but have so far failed to spread outside cultivation. Explanations for many of these failures in naturalization are straightforward: e.g., the species lack tolerance to frost, herbivory, or competition in the new locale; or they reproduce infrequently and irregularly.

The failure of other species introduced repeatedly in the 19th century is not as readily explained (Table 2). A small grass, *Lagurus ovatus* L., was commonly sold for immortelles from 1875 onward because of its attractive panicle. Yet it only sparingly escapes cultivation in the U.S. (Hitchcock 1951). It has however become naturalized elsewhere, such as Cape Province in South Africa (personal observation). *Agrostis nebulosa* Boiss. & Reut. was widely sold for the same purpose and has also failed to become naturalized. Other species in this group represent

interesting parallels with a more successful congener. Both *Bryonia alba* and its congener *B. dioica* Jacq. are vines that die back each winter to a perennial rootstock and produce fleshy, animal-dispersed fruits. Yet only *B. alba* has become invasive in the U.S.

Few of the many eucalypts and acacias introduced into California from Australia have become naturalized: *E. globulus*, *E. polyanthemus* Schauer., *E. teriticornis* Sm. (Table 1). At least 19 others, including *E. leucoxylon* F. Muell., *E. maculata* Hook., *E. robusta* Sm., and *E. saligna* Sm., and five acacias [*A. armata* R. Br. in Ait., *A. dealbata* Link, *A. floribunda* (Vent.) Willd., *A. pycnantha* Benth. in Hook., and *A. suaveolens* (Sm.) Willd.] were repeatedly introduced but do not persist outside cultivation (Table 2). In contrast, some of these unsuccessful immigrants to the U.S. have become invasive weeds in South Africa (e.g., *A. pycnantha*, *A. dealbata*) (Stirton 1983; von Breitenbach 1989) in communities that are similar to the chaparral of California.

Species that fail to become naturalized in the U.S. despite repeated opportunities are potentially powerful tools for unraveling the causes for plant invasions. Experimental comparisons of naturalized species with these "failed aliens" could separate those plant characters that contributed to naturalization compared to those that were merely coincidental. Comparisons among closely-related congeners may be among the most straightforward experimental pairings (Groves 1986), but even a species without an invasive relative represents a decipherable array of traits that singly or collectively precluded its establishment in a new range. Whether plant invasions are simply idiosyncratic and therefore unpredictable events (Crawley 1987), or whether future invasions can be predicted with knowledge of the interactions between the arrays of an immigrant's characters, the features of its new environment, and the circumstances of entry cannot be resolved until we thoroughly examine the species that succeed and those that repeatedly fail in the same new range. The voluminous records provided by these catalogs provide a heretofore unutilized resource in the selection of this experimental material.

RANGE EXPANSION OF NATIVE SPECIES VIA THE SEED TRADE

Seedsmen and nurserymen did not restrict their trade to alien species; as a result, the ranges of

Table 2. Alien species sold in the 19th century that do not or rarely persist outside cultivation in the U.S. Superscripts refer to authorities for nomenclature; species without superscripts are according to Willis (1972). Alternative names that reflect more modern taxonomic treatment are listed in the footnotes.

Catalog Date	Seedsmen Location	Catalog Date	Seedsmen Location	Catalog Date	Seedsmen Location
			<i>Agrostis nebulosa</i> Boiss. & Reuter ^d		<i>Eucalyptus goniocalyx</i> F. Muell. ex Miq. ^b
1824	PA	1860	MA	1886	CA
1826	PA	1869	NY	1898/99	CA
1832	NY	1870	NY		
1862	MA	1875	NY		<i>Eucalyptus haemastoma</i> Sm. ^b
1869	MA (2)	1880	ME; MI; OH		
1898/99	CA	1882	IN		
		1883	IL; NY	1886	CA
		1884	NY; RI	1898/99	CA
		1885	MA		
		1887	IN		<i>Eucalyptus leucoxylon</i> F. Muell.
		1888	NY		
		1890	CA; MI; OR		
		1893	NJ	1895	CA
		1894	IL	1898/99	CA
		1894/95	CA	1899	CA (3)
		1895	MI; NJ		
		1899	OR		<i>Eucalyptus longifolia</i> Link ^b
				1898/99	CA
				1899	CA
					<i>Eucalyptus macrorhyncha</i> F. Muell. ex Benth.
				1886	CA
					<i>Eucalyptus maculata</i> Hook.
				1898/99	CA
					<i>Eucalyptus melliodora</i> A. Cunn. ex Schauer ^b
				1886	CA
				1898/99	CA

Table 2 (Continued)

Catalog Date	Seedsmen Location	Catalog Date	Seedsmen Location	Catalog Date	Seedsmen Location
					<i>L. ovatus</i> (Continued)
				1890	IA; MA
					NY (2); PA
				1893	NJ
				1894	PA
				1894/95	CA
				1895	NJ; NY
					<i>Pittosporum undulatum</i> Vent.
				1826	PA
				1828	PA
				1844/45	PA
				1845	OH
				1862	MA
				1869	MA (2); NY
				1886	CA
				1895	CA
				1899	CA
					<i>Rhododendron ponticum</i> L. ^c
				1811	PA
				1824	PA
				1826	NY; PA
				1828	PA
				1829	NY
				1833	MA (2)
				1841	NY
				1844/45	NY (2); PA
				1846/47	OH
				1847	NY
				1848	OH
				1850/51	MA
				1855	MA
				1863	NY
				1869	NY (2)
					^a Bailey (1949)
					^b Beadle et al. (1972)
					^c Clapham et al. (1987)
					^d Tutin et al. (1980)
					^e equals <i>Bryonia cretica</i> L. subsp. <i>dioica</i> (Jacq.) Tutin (Clapham et al. 1987)

Table 3. Weedy native species that may have undergone range extension by being sold in the 19th century. Superscripts refer to authorities for nomenclature; species without superscripts are according to Fernald (1950).

Catalog Date	Seedsman Location	Catalog Date	Seedsman Location	Catalog Date	Seedsman Location
<i>Asclepias tuberosa</i> L.		<i>Datura stramonium</i> L.		<i>Eupatorium perfoliatum</i> L.	
1804	PA	1807	PA	1875	NY (2)
1826	NY	1875	NY	1885	NY
1829	NY			1888	MA
1831	NY	<i>Echinocystis lobata</i> (Michx.) T. & G.		1890	NY
1833	MA	1859	MA	1899	MA; NY
1835	OH	1869	MA	<i>Eupatorium purpureum</i> L.	
1839	NY	1883	MA	1885	MA
1844/45	NY	1889	MA; NY; OH; OR (2)	<i>Euphorbia corollata</i> L.	
1847	NY			1807	PA
1860	MA	<i>Eschscholtzia californica</i> Cham.		1859	RI
1866	MA	1834/35	MA	1880	NJ; NY
1870	NY	1825	OH	1885	MA
1886	MA	1847	NY	1886	MA
<i>Asclepias verticillata</i> L.		1852	NY	1888	MA (2)
1831	NY	1860	MA	1890	MA
1833	MA	1862	MA	1893	NJ
1839	NY	1863	NY	1895	NJ
1886	MA	1866	NY	1899	IL; MA; NC; NJ; NY (2)
<i>Azolla filiculoides</i> Lam.		1868	MI	<i>Euphorbia heterophylla</i> L.	
1899	PA	1869	MA	1899	MA
<i>Celastrus scandens</i> L.		1870	MA; OH	<i>Galium boreale</i> L.	
1862	PA	<i>Eupatorium</i>		1875	NY
1875	NY	<i>hyssopifolium</i> L.		1885	MA
1883	IL; NY	1885	MA	1888	MA
1884	CA	<i>Eupatorium maculatum</i> L.		1888	MA
1886	NY	1831	NY	<i>Mikania scandens</i> (L.) Willd.	
1890	MI; NY (2)	1839	NY	1835	NY
1895	MI	<i>Cicuta maculata</i> L.		1839	NY
1804	PA			1886	MA
1825	NY				

Table 3 (Continued)

Catalog Date	Seedsman Location	Catalog Date	Seedsman Location
<i>Passiflora incarnata</i> L.		<i>P. cordata</i> (Continued)	
1807	PA	1890	FL; MA;
1828	PA	1899	PA; WI
1845	NY	<i>Sapindus saponaria</i> L. ^a	
1855	MA; PA	1895	FL
1886	PA	<i>Silphium perfoliatum</i> L.	
1888	DC; KY;	1889/90	NY
1889/90	MO; PA	<i>Utricularia vulgaris</i> L.	
	NY	1885	MA
<i>Phlox drummondii</i> Hook.		1888	MA
1855	MA	^a Correll & Johnston (1970)	
1871	MI		
1874	MI		
1875	NY		
1880	MI		
1884	NY		
1888	LA		
1890	LA; MA (2);		
	MI; NY (2);		
	PA (2)		
1894	NY		
1895	MI		
<i>Pistia stratiotes</i> L. ^a			
1884/85	NJ		
1886	PA		
1888	PA		
1889/90	NY		
1890	FL; PA		
1892	FL		
1895	FL; NJ		
1899	KY; MA;		
	NY; PA		
<i>Pontederia cordata</i> L.			
1804	PA		
1807	PA		
1867	MA		
1870	NY		
1884/85	NJ		
1885	MA		
1888	MA; PA		
1889/90	NY		

some species native to North America likely increased (Table 3). Many of these species are either seemingly innocuous or rare, or both, in their new range. *Phlox drummondii* Hook., a native of eastern Texas, is now occasionally found on disturbed sites in the eastern U.S. (Fernald 1950). Others have become weeds of varying severity. *Echinocystis lobata*, native to the eastern U.S., was commonly sold for arbors and its unusual fruit. It is now naturalized in the western U.S. (Correll and Johnston 1970; Welch et al. 1987) and is locally a pest along stream courses. The current ranges of several native aquatic weeds (*Pistia stratiotes* L., *Pontederia cordata* L.) may also reflect dispersal in conjunction with their use as ornamentals. To what extent the putative native ranges of species in the U.S. are partially artifacts of the early trade in their seeds probably cannot be determined. Consequently, it is plausible that a species, especially a ruderal, could have reached a new site and have become well established before it was recognized as naturalized (Smith 1986).

BREEDING PRACTICES AND PLANT FEATURES THAT ENHANCED THE WEEDINESS OF ALIEN SPECIES

Both the practices of seedsmen and the characteristics of the alien species they were disseminating facilitated naturalizations in the 19th century. For instance, repeated transoceanic introductions of plants provide a partial explanation for the difficulty today in controlling some alien weeds (Burdon and Marshall 1981). Given the large native range from which seeds of some species could be gathered, each deliberate introduction probably increased the immigrant's genetic variation and facilitated the production of novel phenotypes in the new range (Barrett 1982). For example, the many multilocus genotypes in *Echium plantagineum* L. in Australia have arisen through the repeated deliberate and accidental introductions of this self-compatible outbreeder (Brown and Burdon 1983; Piggitt 1977). The potential for new phenotypes is further increased if allopatric congeners hybridize, as when brought together in the same nursery. The aggressive shrub *Lantana camara* L. is a polyploid complex that apparently arose in this manner when its non-weedy progenitor species were repeatedly hybridized (Stirton 1977).

Other post-immigration events further influenced the gene pool of these species in their new

range. Even before 1800 the majority of seedsmen were selling material they had produced locally as opposed to serving only as middle men for European sources. Successive growouts year-after-year would have selected for those phenotypes (and eventually races) attuned to the local environment, thereby enhancing the opportunity for establishment if the species escaped from cultivation (Harper 1965).

Most woody species are sold today as potted seedlings or plants grown from cuttings, but in the 19th century most of these species along with herbs and grasses were mailed as seeds. Although such a practice would have operated against the establishment of species with complicated dormancy or a fragile seedling stage, dispersal as seeds offers distinct advantages to a potential invader. Viable seeds are an obviously reliable means for dispersal over great distances. Furthermore, the sale of seeds consciously selected for species that reliably display sexual reproduction, thereby providing a potential source of heterozygosity. The general lack of intensive breeding programs in the 19th century—including the production of sterile hybrids, controlled pollinations, and artificial selection for domestication—meant that these commercial populations were likely to have retained wild characters that enhanced their ability to escape cultivation. For instance, the selection of “double” (and, therefore, usually sterile) flowers was not widely practiced. (An early exception is *Bellis perennis* L.) Unlike accidentally spread seeds, seeds sold through these catalogs were usually sown at high density and cultivated (provided with water, etc.), thereby enhancing the opportunity for these founders to survive, mate, and produce naturalized descendants. The probability for extinction through demographic stochasticity (Lande 1988) for a founder population established in this manner would have been lower than for accidental immigrants.

IMPLICATIONS OF PLANT INTRODUCTIONS IN THE 19TH CENTURY

Information in these 19th century catalogs holds much value for investigating the epidemiology of many plant invasions. (1) Even general knowledge of the geographical distribution of these 19th century seedsmen and the chronology of their businesses is useful in understanding the character and speed of plant inva-

sions. For instance, seed catalogs illustrate the ease with which deliberately introduced species could have spread. (2) In addition to other printed contemporary accounts, herbarium specimens, and fossil pollen spectra (e.g., Davis et al. 1977; Stuckey 1980), seed catalogs are an independent line of evidence as to the time by which an immigrant species had arrived in a new range. The earliest known date(s) of entry provide a time line from which subsequent events in the invasion can be scaled (Forcella and Harvey 1983; Mack 1981). In the case of several prominent alien weeds, such as *Eichhornia crassipes* and *Schinus terebinthifolius*, seed catalogs indicate their arrival earlier than had been previously believed. (3) These records establish a minimum number of points of introduction (and reintroduction) of the invader in the new range; in effect, each seedsmen's garden was a focus for potential spread. (4) Since most seedsmen raised these plants locally, these records provide circumstantial evidence as to the duration and character of selection that occurred in these immigrant populations. (5) Knowing which alien species were repeatedly introduced in the past and yet failed to become naturalized can lead to identifying the plant features that cause plants to fail in a new range.

Despite the prevalence of seed catalogs today, existence of a seed trade industry for over 2 centuries in this country (and much longer in Europe) has not been emphasized in tracing the growth of U.S. agriculture in general (Hedrick 1950; Lawrence 1969; Rehder 1936) or the growth of the alien plant flora in particular. Given the thoroughness with which agents of seed dispersal were compiled earlier in this century and the wide recognition of weeds moving as contaminants in seed lots (Ridley 1930), it is surprising that such an important category of seed dispersal has largely escaped attention. (Common statements in local floras about a species having escaped from cultivation fail to convey any notion of the industry that now seems likely to have transported its progenitors to that site.) Furthermore, information from 19th century seed catalogs has rarely been incorporated into reconstructions of plant invasions (but see Horton 1964; Piggitt 1977). Yet the ease with which seeds, etc. were transported into and throughout the U.S. from at least 1865 onward shows that almost any alien species could have been rapidly and repeatedly introduced into its new range.

Recognition of the pervasiveness of this agency of dispersal throughout the continent complicates any vision of plant invasions operating as simple wave-like or diffusion phenomena (Okubo 1980), except at a local level. With each seedsman serving as a focus for introduction and in turn establishing numerous new foci through his customers, it is little wonder that many alien species appeared from coast to coast within a few years. Consequently, the invasions of the species discussed here likely stemmed from the creation of many small, isolated foci, and this scenario should be considered in any model of the invasion of a deliberately introduced plant (Moody and Mack 1988). Future reconstructions of past invasions will need to consider this agency for dispersal much more than has previously been the case (Foy et al. 1983; Mack 1985, 1986).

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