American Journal of Botany

American Journal of Botany 100(7): 1287–1293. 2013.

SPECIAL INVITED PAPER—GLOBAL BIOLOGICAL CHANGE

Accidental introductions are an important source of invasive plants in the continental United States[1]

Nora E. Lehan[2], Julia R. Murphy[2], Lukas P. Thorburn[3], and Bethany A. Bradley[2,4]

[2]Department of Environmental Conservation, University of Massachusetts, Amherst, Massachusetts 01003 USA; and
[3]Department of Biology, University of Massachusetts, Amherst, Massachusetts 01003 USA

- *Premise of the study:* Preventing new plant invasions is critical for reducing large-scale ecological change. Most studies have focused on the deliberate introduction of nonnatives via the ornamental plant trade. However, accidental introduction may be an important source of nonnative, invasive plants.
- *Methods:* Using Web and literature searches, we compiled pathways of introduction to the United States for 1112 nonnative plants identified as invasive in the continental United States. We assessed how the proportion of accidentally and deliberately introduced invasive plants varies over time and space and by growth habit across the lower 48 states.
- *Key results:* Deliberate introductions of ornamentals are the primary source of invasive plants in the United States, but accidental introductions through seed contaminants are an important secondary source. Invasive forbs and grasses are the most likely to have arrived accidentally through seed contaminants, while almost all nonnative, invasive trees were introduced deliberately. Nonnative plants invading eastern states primarily arrived deliberately as ornamentals, while a high proportion of invasive plants in western states arrived accidentally as seed contaminants. Accidental introductions may be increasing in importance through time. Before 1850, 10 of 89 (11%) of invasive plants arrived accidentally. After 1900, 20 of 65 (31%) arrived accidentally.
- *Conclusions:* Recently enacted screening protocols and weed risk assessments aim to reduce the number of potentially invasive species arriving to the United States via deliberate introduction pathways. Increasing proportions of accidentally introduced invasive plants, particularly associated with contaminated seed imports across the western states, suggest that accidental introduction pathways also need to be considered in future regulatory decisions.

Key words: horticulture; introduction pathway; noxious weed; plant invasion; seed contaminant.

Nonnative, invasive plant species are widely recognized as a major component of global biological change (Vitousek et al., 1996; MA, 2003). Although dozens of invasive plants are ecosystem “transformers” (Richardson et al., 2000) because they alter hydrology, fire regimes, or biogeochemistry, many others impact ecosystems in less pronounced ways. In the large majority of cases, invasive species negatively affect native species (Pyšek et al., 2012). For example, invasive plants often outcompete native plant species and, as a whole, significantly reduce native plant diversity, abundance, and fitness (Vilà et al., 2011). Plant invasions also affect other trophic levels, reducing native animal abundance (Vilà et al., 2011). Invasive plants in agricultural systems (weeds) reduce crop yields and rangeland value and cost farmers in the United States billions of dollars per year to control (Pimentel et al., 2005).

The best way to stop invasive plants and reduce their ecological impacts is to prevent their initial introduction. Once nonnative plants reach the “invasive” stage, defined as species with established populations that are spreading across landscapes or regions with negative ecological impacts (Richardson et al., 2000; Lockwood et al., 2007), they are nearly impossible to eradicate (Rejmánek et al., 2005; Strayer, 2009). Because of the negative impacts of invasive plants, there are clear ecological and economic benefits to preventing their introduction (McAusland and Costello, 2004; Keller et al., 2007) through trade policies (Pheloung et al., 1999; Koop et al., 2012) and early detection of expanding populations (Moody and Mack, 1988).

Nonnative plants are primarily introduced deliberately via the horticulture trade (Reichard and White, 2001). In the eastern United States, the majority of naturalized angiosperms (64% of surveyed species) were introduced deliberately, while only 2% arrived accidentally as seed contaminants and the introduction pathways for the remaining species were unknown (Mack and Erneberg, 2002). In Australia, 94% of nonnative plants were deliberately introduced for gardening, while less than 4% arrived accidentally (Virtue et al., 2004). In Britain, Dehnen-Schmutz et al. (2007) showed that low prices and availability of ornamentals in the 19th and 20th centuries were a strong predictor of the current range of nonnative plants. Increasing trade and demand for ornamentals are likely to continue to increase novel horticultural introductions (Hulme, 2009; Drew et al., 2010; Bradley et al., 2012). Although there are a number of known examples of invasive plants introduced

[1]Manuscript received 11 February 2013; revision accepted 24 May 2013.

The authors thank J. Finn, A. Sakai, and three anonymous reviewers for suggestions that improved this manuscript. This research was supported by the Department of Defense through the Strategic Environmental Research and Development Program (SERDP; grant no. RC-1722) and the National Institute of Food and Agriculture, U. S. Department of Agriculture, the Massachusetts Agricultural Experiment Station, and the Department of Environmental Conservation under Project No. MAS00410.

[4]Author for correspondence (e-mail: bbradley@eco.umass.edu), phone: 413 545 1764, fax: 413 545 4358

doi:10.3732/ajb.1300061

accidentally through contaminated seeds, in hay bales, or attached to livestock, accidental introductions have generally been considered a minor source of nonnative, invasive plants relative to deliberate introductions (NRC, 2002; Mack, 2003).

But, are accidental introductions only a minor pathway of plant invasions? Mack and Erneberg's (2002) estimates for the United States are based on introduction pathways of naturalized angiosperms; naturalized was defined as plant species "that persist without aid of recurring human cultivation" (p.177). Their focus on flowering plants might overestimate the proportion of species introduced via horticulture, as might their broader analysis of all naturalized species vs. only those considered invasive ("invasive" requires that a naturalized species is also spreading across landscapes and regions with negative ecological impacts; Lockwood et al., 2007). In Australia, a survey of nonnative plants showed that approximately 5% of deliberately introduced ornamental plants (1366 of 25 360) went on to become invasive, while an estimated 76% of accidentally introduced plants (141 of 207) became invasive (Virtue et al., 2004). Many more species are deliberately introduced as ornamentals, but accidentally introduced species may be more likely to become invasive (Virtue et al., 2004).

In response to the large numbers of deliberately introduced plant species that go on to become invasive, several authors have suggested ways of decreasing this pathway. Suggestions include horticulture industry self-regulation to reduce the sale of invasive plants (Baskin, 2002; Mack, 2005), educating consumers to support native species cultivation (Drew et al., 2010), and reducing risky imports through regulation or taxation (Perrings et al., 2005; Lodge et al., 2006). Australia has used a weed risk assessment (Pheloung et al., 1999) for over a decade as a decision-making tool for rejecting imports of potentially invasive plants. In the United States, the Animal and Plant Health Inspection Service (APHIS) branch of the U. S. Department of Agriculture has recently initiated a similar screening protocol for horticultural imports (Koop et al., 2012), which has support among industry professionals (Barbier et al., 2013).

APHIS, in collaboration with Customs and Border Protection, also screens a small percentage of cargo imports at international ports for accidental introductions of invasive species. These inspections primarily target insects or pathogens (Magarey et al., 2009), although seeds and other plant parts of federally listed noxious weeds are also a priority (NRC, 2002). Seed imports are also subject to screening under the Federal Seed Act, which prohibits the import of seeds of known noxious weeds and requires that seed shipments be labeled with weed content (Wadley, 1982). Because only several dozen noxious weeds are federally listed (USDA-NRCS, 2012), these regulations target only a small subset of potentially problematic species. For noxious weeds already present in the United States, this "black list" approach is unlikely to be effective for preventing the next wave of invasive species. Current screening policy cannot prevent potentially invasive plant species that are not on the federal noxious weed list from arriving as seed contaminants.

To better understand how invasive plants arrived in the United States and identify future risk, we need a more focused assessment of the pathways of nonnative, invasive plant introduction. Here, we identify introduction pathways for all nonnative plants that have been classified as ecologically important invasives and/or noxious weeds in the continental United States. We hypothesize that pathways for invasive plants will contain a larger proportion of accidental introductions than previously reported pathways of introduction for naturalized plants (Mack and Erneberg, 2002). We further hypothesize that the proportion of species introduced accidentally will increase through time (potentially linked to increasing trade; Hulme, 2009) will vary between plant growth habit (with grasses and forbs more likely to be accidentally introduced as seed contaminants) and will be higher in the western United States (due to larger use of seeds for agricultural and rangeland purposes).

MATERIALS AND METHODS

We created a comprehensive list of all nonnative, invasive plants with known negative impacts on managed systems and/or natural ecosystems in the continental United States (n = 1112) as well as a subset of these invasive plants identified as noxious weeds (n = 403). Invasive plants included all nonnative plants identified as noxious weeds in the USDA PLANTS database (USDA-NRCS, 2012) and/or as invasive plants by the Invasive Plant Atlas of the United States (IPA, 2012). We excluded any species introduced only in Hawaii or Alaska to focus specifically on plants invading the lower 48 states. The full data set can be found in Appendix S1 (see Supplemental Data with the online version of this article).

State and/or federal noxious weeds were identified using the USDA PLANTS database (USDA-NRCS, 2012). The term noxious weed refers to plant species that have been designated by one or more states or the federal government as "undesirable, noxious, harmful, exotic, unjurious, or poisonous, pursuant to State or Federal law" (U. S. Congress, 1974, sec. 2814). Declared noxious weeds tend to be species with negative consequences for agriculture and other managed systems, although the majority also have measurable impacts on natural ecosystems. We excluded any noxious weeds identified at only the genus level, as well as any species native to the United States, and removed synonymous species using the Taxonomic Name Resolution Service (TNRS, Boyle et al., 2013). We identified a total of 403 nonnative noxious weeds in the lower 48 states.

Our category of invasive plants included all of the noxious weeds as well as all "exotic" (i.e., of nonnative origin) species identified as invasive in the lower 48 states in The Invasive Plant Atlas of the United States (IPA, 2012). This database identifies invasive plant species "impacting natural areas" in the United States. We removed synonymous species using the TNRS (Boyle et al., 2013). Of the 1017 species listed on the Invasive Plant Atlas of the United States, 308 overlapped with the nonnative noxious weeds. We combined these sources to identify a total of 1112 nonnative invasive plants (including the 403 noxious weeds) in the lower 48 states.

We used extensive online and literature searches to determine the means of initial introduction for the 1112 nonnative, invasive plants to the United States. Information sources included state and federal websites, university extension services, peer-reviewed literature, and agricultural handbooks (Table 1). Pathways of introduction were categorized into deliberate, accidental, or unknown. For example, an online search for autumn olive (*Elaeagnus umbellata*) introduction reveals that the species was deliberately introduced in Ohio in 1830 as an ornamental (http://www.nps.gov/plants/alien/pubs/midatlantic/elum.htm). We treated each category of deliberate, accidental, or unknown as a binary variable with 0 representing no and 1 representing yes. For various breakdowns of the data set (see below), we used these binary values to calculate the mean proportion of introductions falling into each category as well as the 95% confidence intervals about that proportion based on standard error. We used a one-tailed 95% confidence interval to test for significant differences in the mean proportions between groupings that overlapped in a single direction.

We compared our results on introduction pathways to a previous study that assessed introduction pathways for naturalized (but not necessarily invasive) angiosperms in the United States (Mack and Erneberg, 2002) to determine whether introduction pathways differ between naturalized and invasive plant populations. For many species (such as *E. umbellata*), we were also able to identify more precisely the pathway of deliberate or accidental introduction (e.g., deliberately introduced as an ornamental, accidentally introduced as a seed contaminant). Specific pathways of introduction were recorded whenever available and summarized for the invasive plants.

We also recorded the date of introduction for all of the deliberately and accidentally introduced invasive plants where that information was available. We found introduction dates for 242 of the 1112 invasive plants. We compared the proportion of accidental and deliberate introductions through time, using 50-yr increments beginning in 1850 (species with unknown introduction pathways

TABLE 1. Online resources used to identify introduction pathways of invasive plants (all websites accessed February–July 2012).

Source	Website
State databases	
Calflora	http://www.calflora.org/
California Invasive Plant Council	http://www.cal-ipc.org/
Indiana Cooperative Agricultural Pest Survey	http://extension.entm.purdue.edu/CAPS/
Pennsylvania Department of Conservation and Natural Resources	http://www.dcnr.state.pa.us/index.aspx
Tennessee Exotic Plant Pest Council	http://www.tneppc.org/invasive_plants/
Ohio Perennial and Biennial Weed Guide	http://www.oardc.ohio-state.edu/weedguide/
Wisconsin Department of Natural Resources	http://dnr.wi.gov/
Federal databases	
Plant Conservation Alliance's Alien Plant Working Group	http://www.nps.gov/plants/alien/index.htm
USDA Animal and Plant Health Inspection Service	http://www.aphis.usda.gov/
USDA Forest Service Early Detection and Rapid Response System for Invasive Plants	http://www.fs.fed.us/invasivespecies/earlydetection.shtml
USDA Germplasm Resources Information Network	http://www.ars-grin.gov/
USDA Natural Resources Conservation Service	http://www.nrcs.usda.gov/
U.S Geological Survey	http://www.usgs.gov/
U.S National Park Service	http://www.nps.gov/index.htm
University databases	
Alabama Cooperative Extension System	http://www.aces.edu/main/
Colorado State University Extension	http://www.ext.colostate.edu/
New Mexico State University: College of Agricultural, Consumer and Environmental Sciences	http://aces.nmsu.edu/
Oregon State University Extension	http://extension.oregonstate.edu/
Purdue University: Center for New Crops and Plant Products	http://www.hort.purdue.edu/newcrop/
Texas Agrilife Research and Extension Center at Uvalde	http://uvalde.tamu.edu/
University of Arizona Cooperative Extension	http://extension.arizona.edu/
University of California Agriculture and Natural Resources	http://ucanr.edu/
University of Florida: Center for Aquatic and Invasive Plants	http://plants.ifas.ufl.edu/
University of Idaho Extension	http://www.uidaho.edu/extension
University of Maine DigitalCommons@UMaine	http://digitalcommons.library.umaine.edu/
University of Michigan Herbarium	http://www.lsa.umich.edu/herb/default.asp
University of Texas at Austin: Lady Bird Johnson Wildflower Center	http://www.wildflower.org/
University of Washington: Center for Urban Horticulture	http://depts.washington.edu/uwbg/visit/cuh.php
University of Wisconsin: extension, Cooperative Extension	http://www.uwex.edu/ces/
Research databases	
Discover Life	http://www.discoverlife.org/
Food and Agricultural Organization of the United Nations	http://www.fao.org/index_en.htm
Global Invasive Species Database	http://www.issg.org/database/welcome/
Invasive Species Specialist Group	http://www.issg.org/
Invasive.org: Center for Invasive Species and Ecosystem Health	http://www.invasive.org/
iMap Invasives	http://www.imapinvasives.org/GIST/ESA/index.html
IPANE: Invasive Plant Atlas of New England	http://www.eddmaps.org/ipane/
U.S Army Corps of Engineers: Engineer Research and Development Center	http://www.erdc.usace.army.mil/
Books and journals	
Critical Reviews in Plant Sciences	http://www.tandfonline.com/toc/bpts20/current
Grasses Introduced into the United States, Agricultural Handbook No. 48	
Journal of Ecology	http://www.journalofecology.org/
Weed Science	http://www.bioone.org/loi/wees
Weed Technology	http://www.bioone.org/loi/wete

were excluded). Dates for accidental introduction of species were typically much less precise than those for deliberately introduced species because accidental species tend to go unnoticed for many years. Accidental introduction dates tended to be recorded as "early", "mid", or "late" century in the online archives that we searched. We classified "early" and "mid" century introductions as the first half of the century and "late" century introductions as the second half of the century.

Plant growth form (habit) may influence whether species are more likely to be targeted as ornamentals for deliberate introduction or more likely to accidentally contaminate imports. To test whether the proportion of deliberate and accidental introduction is influenced by growth habit, we classified species into five growth habits as defined by the USDA PLANTS website (USDA-NRCS, 2012): forbs/herbs (297 species), grasses (107 species), vines (79 species), shrubs (125 species), and trees (172 species). Aquatic plants (which had only 15 records) and species with unknown introduction sources were excluded.

Given both historical land use and population patterns across the U.S., there may be geographic trends to the proportion of deliberate vs. accidental introductions. For each invasive species, we identified the states where the species is currently recorded as invasive based on the Invasive Plant Atlas and/or state noxious weed lists. The Invasive Plant Atlas (IPA, 2012) includes information from the Early Detection and Distribution Mapping System (EDDMapS) (Center for Invasive Species and Ecosystem Health, 2012), which identifies the states where each species is currently reported as invasive (a subset of the species' total distribution). For invasive plants that are also noxious weeds, we identified the states where each species was declared as a noxious weed (USDA-NRCS, 2012). We used these data to map the percentage of deliberate vs. accidental introductions by state to look for spatial trends in introduction source. Species with unknown introduction pathways were excluded from this analysis.

RESULTS

A total of 1112 nonnative, invasive plants were identified by the Invasive Plant Atlas and/or were on state noxious weed lists. Deliberate introductions account for 671 (60%) of the invasive plants, 126 (11%) were accidentally introduced, and the remaining 315 (28%) had an unknown introduction pathway. The percentages of deliberate and accidental pathways for invasive plants differed significantly from the pathways for naturalized angiosperms (64% and 2% for deliberate and accidental, respectively) measured by Mack and Erneberg (2002) ($\chi^2 = 137.9$, df = 1, $P < 0.001$). For the subset of 403 noxious weeds, 233 (58%) were deliberately introduced, 84 (21%) were accidentally introduced and the remaining 86 (21%) had an unknown introduction pathway (Fig. 1A). The noxious weeds' proportion of deliberate vs. accidental introduction pathways also differed significantly from that of the nonnative angiosperms reported by Mack and Erneberg (2002) ($\chi^2 = 240.7$, df = 1, $P < 0.001$).

Of the deliberately introduced invasive plants, 426 (64%) were introduced for ornamental purposes, 86 (13%) as forage crops, 41 (6%) for environmental restoration, and 33 (5%) for medicinal uses. The remaining 83 (12%) were deliberately introduced for unknown purposes, many of which were also likely ornamental, but were not documented as such in online and literature sources. Of the accidentally introduced invasive plants, 83 (65%) were contaminants of imported seeds, 15 (12%) were transported in ballast water, 8 (6%) were contaminants of other imports (e.g., packaging or livestock), and the remaining 22 (17%) were accidentally introduced via an unknown pathway (Fig. 1B).

The proportion of invasive plants in the United States introduced via the accidental pathway has increased through time (Fig. 2). We found introduction dates for 242 of the 1112 invasive plants. Before 1851, only 10 of 89 species were introduced accidentally (11%). Between 1851 and 1900, 14 of 88 species were introduced accidentally (16%). Between 1901 and 1950, 12 of 48 species were introduced accidentally (25%), and after 1950, 8 of 17 species were introduced accidentally (47%). The fraction of accidental introductions varied significantly over time ($\chi^2 = 14.2$, df = 3, $P < 0.01$), and the average fraction of accidental introductions was significantly higher after 1950 than in the pre-1850 or 1851–1900 periods (one-sided z test, $z = -4.36$, $P < 0.001$; $z = -3.49$, $P < 0.001$, respectively).

The fraction of accidentally introduced species varied significantly by plant growth habit (Fig. 3; $\chi^2 = 76.3$, df = 4, $P < 0.001$, $n = 795$ excluding species with unknown pathways). Trees were the least likely to be accidentally introduced (2 of 172 species, 1%). Shrubs (6 of 125 species, 5%) were also rarely accidentally introduced, but the overall fraction was significantly higher than trees (one-tailed z test; $z = -3.78$, $P <$ 0.001). Vines (8 of 79 species, 10%) had a significantly higher fraction of accidentally introductions than trees and shrubs ($z = -7.41$, $P < 0.001$; $z = -2.2$, $P = 0.014$, respectively). Grasses (26 of 107 species, 24%) and forbs/herbs (81 of 297 species, 28%) were the most likely to be accidentally introduced and had a significantly higher fraction of accidental introductions

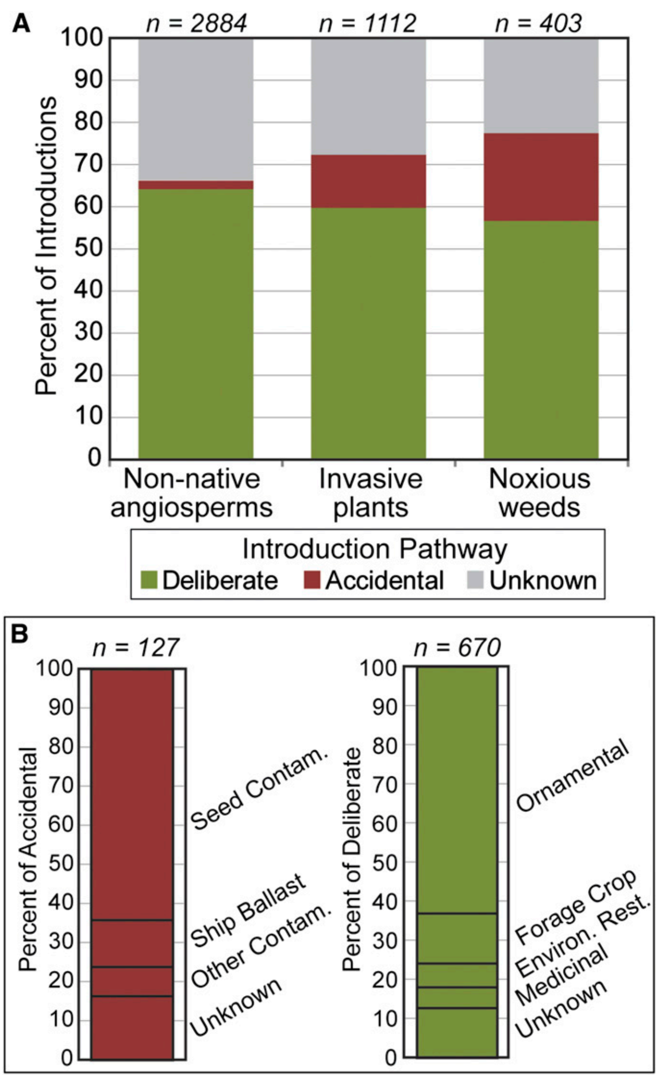

Fig. 1. Pathways of invasive plant introductions to the continental United States. (A) The majority of nonnative angiosperms were deliberately introduced via the ornamental plant trade, with only 2% arriving accidentally (data from Mack and Erneberg, 2002). For nonnative, invasive plants, 11% were accidentally introduced, while for the subset of noxious weeds, 21% were accidentally introduced. (B) Specific introduction pathways for accidentally and deliberately introduced invasive plants. Contaminated seeds are the primary means of accidental introduction; the ornamental plant trade is the primary means of deliberate introduction.

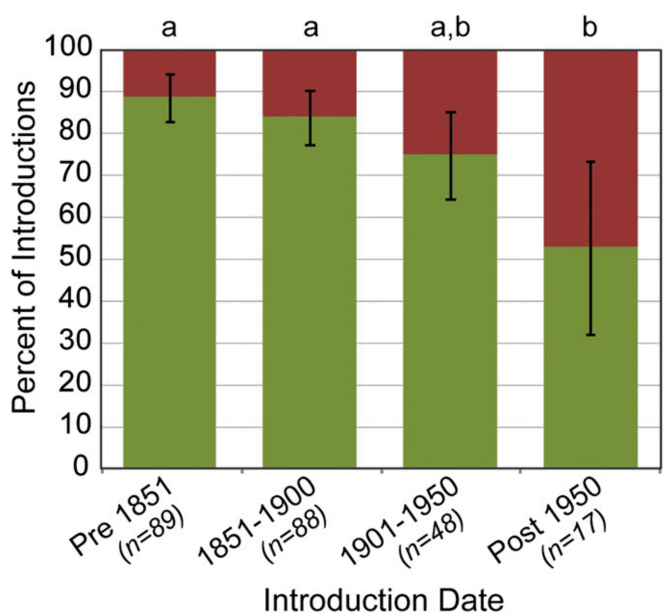

Fig. 2. Accidental introductions have become an increasingly important source of invasive plant introductions through time. Red bars: accidental introduction, green bars: deliberate introduction. Error bars show the 95% confidence interval about the mean, and different letters above the bars indicate a significant difference in the means based on one-tailed distributions at the 95% confidence interval.

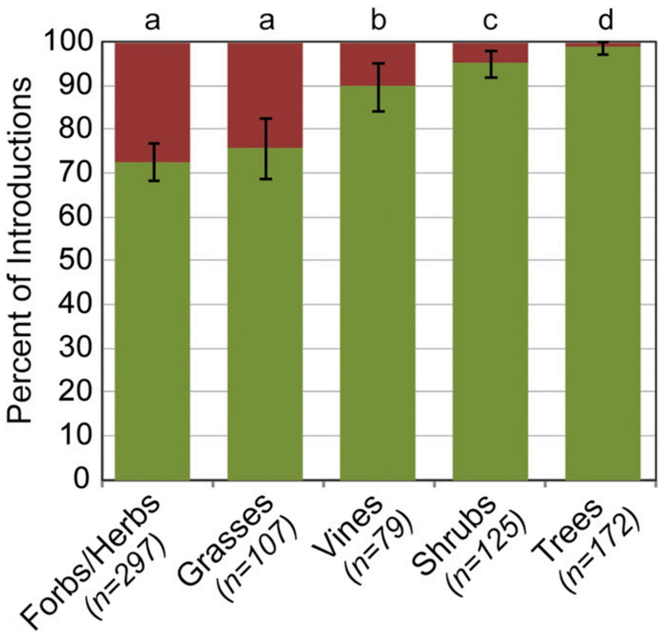

Fig. 3. Introduction pathways vary considerably by plant growth habit. Although all types of invasive plants are more likely to have been deliberately introduced, a significantly larger percentage of forbs and grasses were accidentally introduced than vines, shrubs and trees. Red bars: accidental introduction, green bars: deliberate introduction. Error bars show the 95% confidence interval about the mean, and different letters above the bars indicate a significant difference in the means based on one-tailed distributions at the 95% confidence interval.

than vines, shrubs, and trees ($z = -10.25$, $P < 0.001$; $z = -19.42$, $P < 0.001$, respectively).

The proportion of accidental vs. deliberate introduction source varied substantially by state (Fig. 4). Plants identified as invasive within eastern states have much lower proportions of accidental introductions than in western states. In nine states, seven of which are east of the Mississippi River, less than 10% of plants identified as invasive were introduced accidentally. Conversely, more than 40% of plants identified as invasive were introduced accidentally in eight states, all of which are west of the Mississippi River, with 53% (25 of 47) introduced accidentally in Idaho and 51% (20 of 39) in South Dakota.

DISCUSSION

Invasive plants in the United States have been introduced primarily through the ornamental plant trade (Fig. 1). This pattern mirrors the introduction pathways of naturalized species (nonnative, but not necessarily invasive plants), which are also primarily introduced as ornamentals (Mack and Erneberg, 2002; Virtue et al., 2004; Lambdon et al., 2008). Because they are deliberately cultivated, ornamentals are less likely to suffer from failures at the transport, introduction, and establishment stages of invasion (Richardson et al., 2000; Lockwood et al., 2007; Blackburn et al., 2011).

To prevent the next wave of deliberately introduced invasive plants, previous studies have focused on closing the ornamental plant pathway (Perrings et al., 2005; Lodge et al., 2006). Weed risk assessments have been applied in numerous countries with overall high levels of accuracy in discriminating invasive from noninvasive plant species (Pheloung et al., 1999; Gordon et al., 2008; McClay et al., 2010) and strong economic benefits (Keller et al., 2007). Recently, the U. S. Department of Agriculture's Animal and Plant Health Inspection Service (APHIS) has begun labeling high risk species as Not Authorized Pending Pest Risk Analysis (NAPPRA) until they can be cleared by a weed risk assessment (Koop et al., 2012). This approach should go far toward closing the ornamental introduction pathway. However, current regulations are not sufficient for reducing the accidental introduction pathway.

Accidental introductions are the source of at least 12% of all invasive plants in the United States and 21% of the noxious weeds. These numbers are likely underestimates because we

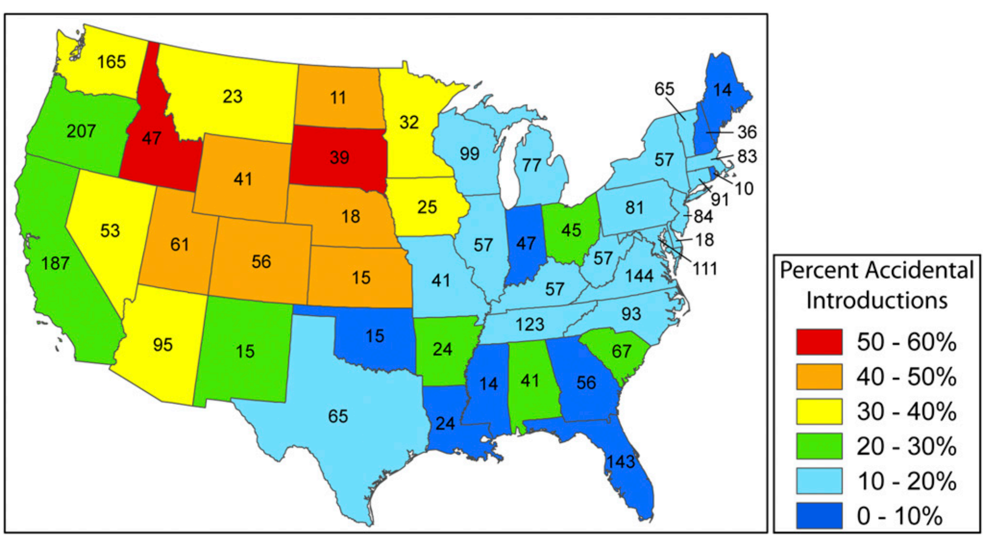

Fig. 4. Percentage of known invasive plant introduction pathways that were accidental for each state. Numbers represent the total count of invasive plants with known introduction pathways identified in each state. Warmer colors indicate more accidental introduction pathways, primarily seed contaminants, and are clustered in the western United States. Cooler colors indicate more deliberate introduction pathways, primarily ornamentals, and are clustered in the eastern United States.

were unable to find introduction source information for nearly a third (28%) of the invasive species. Information on deliberate introductions was more likely to be recorded and therefore easier to find than for accidental introductions, so it is likely that accidental introductions are disproportionately represented in this unknown category.

Seed contaminants account for the majority of accidental introductions and are the second largest single source of invasive plants in the United States after ornamentals. The proportion of accidental introductions of invasive plant species has been growing with time (Fig. 2). Although seed contaminants do not have the same advantage as ornamentals of being deliberately transported and cultivated, they are likely to have been planted along with cultivated crops. Widespread planting alongside crops might give seed contaminants the chances they need to overcome barriers to invasion (e.g., Blackburn et al., 2011). For example, a study of seed imports into Alaska showed that an average kilogram of crop seeds contained the seeds of six additional species and nearly 4000 contaminant seeds (Conn, 2012). Expanded seed trade in later time periods and imports of contaminated seed from novel trading partners creates further opportunities for accidental introductions. The increasing proportion of invasive plants introduced as seed contaminants suggests that the accidental pathway may be an important source of introductions today for species that will go on to become invasive in the future after a lag period (Mack et al., 2000; Essl et al., 2011). If the late 20th century rates of accidental introduction are an accurate reflection of current introduction pathways, then seed contaminants will likely be a more important source for future invasive plants than data from earlier time periods would suggest.

Forbs and grasses are significantly more likely than vines, shrubs or trees to be introduced accidentally (Fig. 3). Given that seed contaminants are the primary source of accidental introductions for terrestrial species, it is likely that many of these forbs and grasses were weedy species able to take advantage of disturbance and additional resources available in crop fields (Barrett, 1983). Importing contaminated crop and grass seeds may create an unintentional filter (Alpert, 2006) that increases the likelihood of accidentally introducing weedier plant seeds. Examples of forbs introduced as seed contaminants include some of the most widespread and problematic species across the West and Midwest: *Acroptilon repens*, *Centaurea solstitialis*, *Chondrilla juncea*, *Cirsium arvense*, *Lepidium latifolium*. This hypothesis is supported by the spatial distribution of accidental introductions across the United States (Fig. 4). Accidental introductions via seed contaminants are most likely in western states, particularly those more focused on agricultural and rangeland production.

International trade regulations currently do little to prevent the introduction of novel plant species in seeds (Perrings et al., 2010). For example, a recent analysis of one 50-kg shipment of spring wheat seeds from Canada to Japan contained 40 different weed species despite relatively stringent grain shipment protocols in Canada (Shimono and Konuma, 2008). Seed imports to the United Sates are required to be labeled with estimated weed content, and imports of federally recognized noxious weeds are prohibited (Wadley, 1982). However, this regulation only prevents the import of selected invasive plant species that have already arrived. Many invasive plants that will affect ecosystems in the future have not yet arrived, but globalization increases the chances for their introduction (Hulme, 2009). Current import regulations do not address the accidental introduction pathway for invasive plants.

Although proactive inspection and treatment of cargo imports may be effective for treating pests and pathogens (Campbell, 2001; Magarey et al., 2009), the same is unlikely to be true for seed imports. Any process that sterilizes seed contaminants is likely to be equally detrimental to the primary seed crop. Instead, accidental introduction pathways are more likely to be addressed through international trade regulations that aim to reduce cargo and seed contamination (McNeely, 2006; Perrings et al., 2010). Global databases of invasive species (Meyerson and Mooney, 2007), including keys for identifying their seeds, would help APHIS to identify and quarantine problematic shipments, but only given the appropriate regulatory capacity for this action. Screening of seed imports could focus on shipments originating from countries with less extensive trade histories with the United States because novel plant species are likely to be introduced at the highest rates during the early stages of trade partnerships (Levine and D'Antonio, 2003; Bradley et al., 2012).

LITERATURE CITED

ALPERT, P. 2006. The advantages and disadvantages of being introduced. *Biological Invasions* 8: 1523–1534.

BARBIER, E. B., D. KNOWLER, J. GWATIPEDZA, S. H. REICHARD, AND A. R. HODGES. 2013. Implementing policies to control invasive plant species. *BioScience* 63: 132–138.

BARRETT, S. 1983. Crop mimicry in weeds. *Economic Botany* 37: 255–282.

BASKIN, Y. 2002. The greening of horticulture: New codes of conduct aim to curb plant invasions. *BioScience* 52: 464–471.

BLACKBURN, T. M., P. PYSEK, S. BACHER, J. T. CARLTON, R. P. DUNCAN, V. JAROSIK, J. R. U. WILSON, ET AL. 2011. A proposed unified framework for biological invasions. *Trends in Ecology & Evolution* 26: 333–339.

BOYLE, B., N. HOPKINS, Z. LU, J. A. R. GARAY, D. MOZZHERIN, T. REES, N. MATASCI, ET AL. 2013. The taxonomic name resolution service: An online tool for automated standardization of plant names. *BMC Bioinformatics* 14: 16.

BRADLEY, B. A., D. M. BLUMENTHAL, R. EARLY, E. D. GROSHOLZ, J. J. LAWLER, L. P. MILLER, C. J. B. SORTE, ET AL. 2012. Global change, global trade, and the next wave of plant invasions. *Frontiers in Ecology and the Environment* 10: 20–28.

CAMPBELL, F. T. 2001. The science of risk assessment for phytosanitary regulation and the impact of changing trade regulations. *BioScience* 51: 148–153.

CENTER FOR INVASIVE SPECIES AND ECOSYSTEM HEALTH. 2012. EDDMapS: Early Detection & Distribution Mapping System. Available at http://www.eddmaps.org/. Center for Invasive Species and Ecosystem Health, University of Georgia, Athens, Georgia, USA.

CONN, J. S. 2012. Pathways of invasive plant spread to Alaska: III. Contaminants in crop and grass seed. *Invasive Plant Science and Management* 5: 270–281.

DEHNEN-SCHMUTZ, K., J. TOUZA, C. PERRINGS, AND M. WILLIAMSON. 2007. A century of the ornamental plant trade and its impact on invasion success. *Diversity & Distributions* 13: 527–534.

DREW, J., N. ANDERSON, AND D. ANDOW. 2010. Conundrums of a complex vector for invasive species control: A detailed examination of the horticultural industry. *Biological Invasions* 12: 2837–2851.

ESSL, F., S. DULLINGER, W. RABITSCH, P. E. HULME, K. HULBER, V. JAROSIK, I. KLEINBAUER, ET AL. 2011. Socioeconomic legacy yields an invasion debt. *Proceedings of the National Academy of Sciences USA* 108: 203–207.

GORDON, D. R., D. A. ONDERDONK, A. M. FOX, AND R. K. STOCKER. 2008. Consistent accuracy of the Australian weed risk assessment system across varied geographies. *Diversity & Distributions* 14: 234–242.

HULME, P. E. 2009. Trade, transport and trouble: Managing invasive species pathways in an era of globalization. *Journal of Applied Ecology* 46: 10–18.

IPA. 2012. Invasive plant atlas of the United States. Available at http://www.invasiveplantatlas.org/ [accessed June, 2012]. University of Georgia,– Center for Invasive Species and Ecosystem Health, Athens, Georgia, USA and the National Park Service, Washington, D.C., USA.

KELLER, R. P., D. M. LODGE, AND D. C. FINNOFF. 2007. Risk assessment for invasive species produces net bioeconomic benefits. *Proceedings of the National Academy of Sciences USA* 104: 203–207.

KOOP, A., L. FOWLER, L. NEWTON, AND B. CATON. 2012. Development and validation of a weed screening tool for the United States. *Biological Invasions* 14: 273–294.

LAMBDON, P. W., F. LLORET, AND P. E. HULME. 2008. How do introduction characteristics influence the invasion success of Mediterranean alien plants? *Perspectives in Plant Ecology, Evolution and Systematics* 10: 143–159.

LEVINE, J. M., AND C. M. D'ANTONIO. 2003. Forecasting biological invasions with increasing international trade. *Conservation Biology* 17: 322–326.

LOCKWOOD, J., M. HOOPES, AND M. MARCHETTI. 2007. Invasion ecology. Blackwell, Malden, Massachusetts, USA.

LODGE, D. M., S. WILLIAMS, H. J. MACISAAC, K. R. HAYES, B. LEUNG, S. REICHARD, R. N. MACK, ET AL. 2006. Biological invasions: Recommendations for US policy and management. *Ecological Applications* 16: 2035–2054.

MA [MILLENIUM ECOSYSTEM ASSESSMENT]. 2003. Ecosystems and human wellbeing: A framework for assessment. Island Press, Washington, D.C., USA.

MACK, R. N. 2003. Global plant dispersal, naturalization and invasion: Pathways, modes and circumstances. *In* G. M. Ruiz and J. T. Carlton [eds.], Invasive species: Vectors and management strategies, 3–30. Island Press, Washington, D.C., USA.

MACK, R. N. 2005. Predicting the identity of plant invaders: Future contributions from horticulture. *HortScience* 40: 1168–1174.

MACK, R. N., AND M. ERNEBERG. 2002. The United States naturalized flora: Largely the product of deliberate introductions. *Annals of the Missouri Botanical Garden* 89: 176–189.

MACK, R. N., D. SIMBERLOFF, W. M. LONSDALE, H. EVANS, M. CLOUT, AND F. A. BAZZAZ. 2000. Biotic invasions: Causes, epidemiology, global consequences, and control. *Ecological Applications* 10: 689–710.

MAGAREY, R. D., M. COLUNGA-GARCIA, AND D. A. FIESELMANN. 2009. Plant biosecurity in the United States: Roles, responsibilities, and information needs. *Bioscience* 59: 875–884.

MCAUSLAND, C., AND C. COSTELLO. 2004. Avoiding invasives: Trade-related policies for controlling unintentional exotic species introductions. *Journal of Environmental Economics and Management* 48: 954–977.

MCCLAY, A., A. SISSONS, C. WILSON, AND S. DAVIS. 2010. Evaluation of the Australian weed risk assessment system for the prediction of plant invasiveness in Canada. *Biological Invasions* 12: 4085–4098.

MCNEELY, J. A. 2006. As the world gets smaller, the chances of invasion grow. *Euphytica* 148: 5–15.

MEYERSON, L. A., AND H. A. MOONEY. 2007. Invasive alien species in an era of globalization. *Frontiers in Ecology and the Environment* 199–208.

MOODY, M. E., AND R. N. MACK. 1988. Controlling the spread of plant invasions—The importance of nascent foci. *Journal of Applied Ecology* 25: 1009–1021.

NRC [NATIONAL RESEARCH COUNCIL]. 2002. Predicting invasions by nonindigenous plants and plant pests, 198. National Academies Press, Washington, D.C., USA.

PERRINGS, C., S. BURGIEL, M. LONSDALE, H. MOONEY, AND M. WILLIAMSON. 2010. International cooperation in the solution to trade-related invasive species risks. *Annals of the New York Academy of Sciences* 1195: 198–212.

PERRINGS, C., K. DEHNEN-SCHMUTZ, J. TOUZA, AND M. WILLIAMSON. 2005. How to manage biological invasions under globalization. *Trends in Ecology & Evolution* 20: 212–215.

PHELOUNG, P. C., P. A. WILLIAMS, AND S. R. HALLOY. 1999. A weed risk assessment model for use as a biosecurity tool evaluating plant introductions. *Journal of Environmental Management* 57: 239–251.

PIMENTEL, D., R. ZUNIGA, AND D. MORRISON. 2005. Update on the environmental and economic costs associated with alien-invasive species in the United States. *Ecological Economics* 52: 273–288.

PYŠEK, P., V. JAROŠÍK, P. E. HULME, J. PERGL, M. HEJDA, U. SCHAFFNER, AND M. VILÀ. 2012. A global assessment of invasive plant impacts on resident species, communities and ecosystems: The interaction of impact measures, invading species' traits and environment. *Global Change Biology* 18: 1725–1737.

REICHARD, S. H., AND P. WHITE. 2001. Horticulture as a pathway of invasive plant introductions in the United States. *Bioscience* 51: 103–113.

REJMANEK, M., D. M. RICHARDSON, S. I. HIGGINS, M. J. PITCAIRN, AND E. GROTKOPP. 2005. Ecology of invasive plants: State of the art. *In* H. A. Mooney, R. N. Mack, J. A. McNeeley, L. E. Neville, P. J. Schei, and J. K. Waage [eds.], Invasive alien species: A new synthesis, 104–161. Island Press, Washington, D.C., USA.

RICHARDSON, D. M., P. PYSEK, M. REJMANEK, M. G. BARBOUR, F. D. PANETTA, AND C. J. WEST. 2000. Naturalization and invasion of alien plants: Concepts and definitions. *Diversity & Distributions* 6: 93–107.

SHIMONO, Y., AND A. KONUMA. 2008. Effects of human-mediated processes on weed species composition in internationally traded grain commodities. *Weed Research* 48: 10–18.

STRAYER, D. L. 2009. Twenty years of zebra mussels: Lessons from the mollusk that made headlines. *Frontiers in Ecology and the Environment* 7: 135–141.

U. S. CONGRESS. 1974. Federal Noxious Weed Act, sec. 2814, Management of undesirable plants on Federal lands. Available at http://www.aphis.usda.gov/plant_health/plant_pest_info/weeds/downloads/sec2814.pdf.

USDA-NRCS. 2012. The PLANTS Database. Available at http://plants.usda.gov [accessed February 2012]. National Plant Data Center, Baton Rouge, Louisiana, USA.

VILÀ, M., J. L. ESPINAR, M. HEJDA, P. E. HULME, V. JAROŠÍK, J. L. MARON, J. PERGL, ET AL. 2011. Ecological impacts of invasive alien plants: A meta-analysis of their effects on species, communities and ecosystems. *Ecology Letters* 14: 702–708.

VIRTUE, J. G., S. J. BENNETT, AND R. P. RANDALL. 2004. Plant introductions in Australia: How can we resolve "weedy" conflicts of interest? *In* B. M. Sindel and S. B. Johnson [eds.], Proceedings of the 14th Australian Weeds Conference, Sydney, Australia, 42–48. Weeds Society of New South Wales, Wahroonga, New South Wales, Australia.

VITOUSEK, P. M., C. M. D'ANTONIO, L. L. LOOPE, AND R. WESTBROOKS. 1996. Biological invasions as global environmental change. *American Scientist* 84: 468–478.

WADLEY, J. B. 1982. The Federal Seed Act: Regulation of seed sales and remedies available to the seed purchaser. *South Dakota Law Review* 27: 453–475.