Sego Lily
Newsletter of the Utah Native Plant Society
September 2011 (volume 34 number 5)

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*Cover: Common purslane (*Portulaca oleracea*) occurs worldwide in weedy habitats, but does that make it non-native? For the answer, see page 5. Photo by Al Schneider (www.swcoloradowildflowers.com).*

Determining the Nativity of Plant Species

By Walter Fertig

Competition from invasive, non-native plant and animal species is considered the second greatest threat to biological diversity in the United States after habitat loss. An estimated 5000 plant species have been deliberately or accidentally introduced into the United States over the last five centuries. Of these, about 500 are considered serious agricultural pests. Pimental et al. (2000) estimate that reduced crop yields and expenses for the control of invasive weedy plants cost the US agricultural economy $26.4 billion per year. Invasive non-native species also impact native plant species and communities through direct competition, altered fire regimes, and reduced habitat quality and complexity. Control of non-natives has become an increasingly important task of land managers, siphoning away money and resources that might be better put towards other conservation issues.

Given the importance of non-native plant species, surprisingly little attention has been paid to how nativity is actually determined (Willis & Birks 2006). Typically, plant taxa are considered native if they are found within their presumed area of evolutionary origin, or arrived without human intervention (Pysek et al. 2004). Non-natives, by contrast, are known or suspected to have been brought to a new area by humans on purpose (to be grown for food, fiber, or ornamentation) or to have escaped by accident. Most introductions fail to become [continued on page 4]

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Sego Lily Editor: Walter Fertig (walt@kanab.net). The deadline for the November 2011 *Sego Lily* is 15 October 2011.

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Chapter News

Fremont (Richfield area): The Fremont Chapter had a busy summer! For June's presentation, local photographer Kreig Rasmussen shared tips on how to get great pictures. It was a great session, and everyone came away with a few more tricks for getting amazing photos. In July, chapter members had a campout at the cabin up Seven Mile to enjoy native plants in their world. Our members are also constantly working to maintain our native plant gardens at Fremont Indian State Park and the Sevier County Administration Building.

The Fremont Chapter is still looking to get back into the calendar-making business as a fundraiser—we still have some spots for various chapters' photos, but we'd like to get the calendar into final production AS SOON AS POSSIBLE in order to allow holiday sales. For any questions, or to submit your high-resolution photo and information, please contact Janett Warner at janettwildland@gmail.com .

On a sad note, one of our long-time chapter members, Elissa Jean Wood Stevens, passed away on July 31, 2011, from complications due to pancreatic cancer.—*Lisa White*

Manzanita (Kane County): For our August adventure, the chapter visited the organic farm of John and Rhonda Flatberg along the Virgin River, just north of Glendale. The Flatbergs have spent over two decades slowly restoring a degraded wet meadow through rest and rotation of a small herd of cattle. They have also constructed several solar-heated structures and greenhouses and are living completely off the grid. Attendees got to admire the construction and also tromp about the wet meadow and riparian vegetation to admire the late summer flora.

Our next event will be an evening hike in Kanab Creek Canyon on the premises of the Best Friends Animal Sanctuary on Tuesday, September 13 from 6:30-dusk. Participants will be invited to help locate new species for the sanctuary plant list, currently being developed by your chapter's umbel leader. Please meet at the Best Friends Welcome Center parking lot at 6:15 to then get going at 6:30.—*W. Fertig*

Bulletin Board

UNPS Annual Meeting, 5 November 2011: The Salt Lake Chapter will be hosting the annual Utah Native Plant Society members meeting and potluck on Saturday, November 5 at Red Butte Garden from 1-5 PM. Past Society President Bill Gray will address the group about his project to catalogue and relocate photo points in Utah and the southwest taken by pioneer botanist and noted curmudgeon Marcus E. Jones. Dr. Gray's work has been funded, in part, through a small grant from UNPS. The meeting will also include the election of new society officers and board members and is an excellent opportunity to socialize with kindred native plant lovers.

Herbarium Meeting: The Intermountain Herbarium of Utah State University in Logan is hosting the annual regional meeting of western herbaria this fall from September 30-October 2. The meeting will include updates on the activities of various herbaria in the region and ongoing efforts to develop a regional consortium of collections and present herbarium data digitally on the internet. Dr. John Spence, expert bryologist from Glen Canyon National Recreation Area, will lead a field trip and workshop focusing on the identification of bryophytes. For additional information, contact Dr. Michael Piep, assistant curator of the Intermountain Herbarium (Michael.piep@usu.edu).

Pollinator Conservation Talk, 12 September 2011: Bees and other pollinators are a fundamental part of our environment. There are more than 4000 native bee species in North America, and their work is something that touches us all through the food we eat, the clothes we wear, and the landscapes we enjoy, and yet their future is clouded by habitat loss, pesticide use, and introduced diseases.

Join Mace Vaughan, Pollinator Program Director of the Xerces Society and Joint Pollinator Conservation Specialist for the USDA's Natural Resources Conservation Service, and coauthor of the newly released book, *Attracting Native Pollinators*, to learn more about the fascinating lives of these insects and glean information about how you can care for these vital animals where you live. Whether you are an urban gardener, a suburban park manager, a working farmer, or just care about where your food comes from, this evening has something for you. The meeting will be at the Gore Auditorium of Westminster College in Salt Lake City on Monday, September 12 from 7:30 to 9 PM. Admission is free and parking available under the athletic field off 1700 South.

Pollinator Workshops: The Xerces Society is also sponsoring two one-day courses in Pollinator Conservation Planning in St. George (Weds., September 14) and Richfield (Thurs., September 15) by Mace Vaughan. These classes will equip conservationists, land managers, farm educators, and agricultural professionals with the latest science-based approaches to increasing crop security and reversing the trend of pollinator decline, especially in heavily managed agricultural landscapes. To register, click on the Xerces Society webpage (http://www.xerces.org/events/).

Salt Lake Chapter: The next meeting of the SL Chapter will focus on UFOs—unidentified flowering objects! Bill Gray will be the master of ceremonies, but needs your help with submissions of UFO images at least one week prior to the meeting. UFO night will be Wednesday, September 7 at 7 PM at the Salt Lake City REI (3285 E 3300 South). Admission is free and open to all.

Right: An Unidentified Flowering Object observed by Bill King in southern Nevada in late winter. Can you guess what this plant is or its planet of origin? Answer in the next issue.

Determining the Nativity of Plant Species

(Continued from page 1)

established or naturalized without further human assistance and occur only in cultivated settings. Decisions about nativity have traditionally been made by the authors of regional floras, often without providing a rationale.

Determining the nativity of two small subsets of plant taxa is especially problematic. The first group includes species that are widely disjunct from the core area of their range. Disjunctions can arise naturally by long-distance dispersal or vicariance (contraction and isolation of once continuous ranges). In some instances, native Americans may have augmented the spread of species before European contact, as in the cases of maize (*Zea mays*), kidney beans, (*Phaseolus vulgaris*), and various squashes (*Cucurbita* spp.). The second group is composed of weedy species that commonly occur in disturbed habitats and have been known since very early in the European colonization of the world. This group includes some cosmopolitan weeds, such as purslane (*Portulaca oleracea*), common reedgrass (*Phragmites australis*), and Kentucky bluegrass (*Poa pratensis*), as well as such North American "weeds" as bug-seed (*Corispermum* spp.), ragweed (*Ambrosia* spp.), and biennial wormwood (*Artemisia biennis*).

Incorrectly determining the native status of a species can have serious ramifications. Native disjunct species are often rare and of conservation interest as these isolated populations are potential sources of speciation and vulnerable to chance extinction events. If misidentified as non-native, these populations might be subjected to weed control efforts or ignored when they could benefit from benevolent stewardship.

To reduce this uncertainty, Webb (1985) recommended eight criteria for assessing the nativity of a species. These criteria include: fossil evidence (pollen and macrofossils), historical data (herbarium records, floristic checklists, historic literature), geographic distribution, frequency of known naturalization, genetic diversity, reproductive pattern (asexual or human-mediated vs. sexual or unmediated), and possible means of introduction. Few of these are definitive by themselves, but taken together they can provide evidence that a given species is native or introduced. I will apply each of Webb's criteria to specific case studies from the putative non-native flora of North America. My focus will primarily be on species affected by European contact, rather than on "archaeophytes" that were transported widely by humans in Pre-Columbian times.

*Above: Yellow bee plant (*Cleome lutea *or* Peritoma lutea*) is a native North American wildflower that commonly occurs in weedy habitats and might, therefore, be mistaken for being non-native. Fossil remains of bee plant pollen and seeds from pre-Columbian archaeological sites provides solid evidence that* Cleome *species are truly native to North America. Photo by Al Schneider (www.swcoloradowildflowers.com).*

Fossil Evidence

Reliably dated and identified fossils provide the most concrete evidence that a plant species was present in an area prior to European contact, and thus native. Unfortunately, fossil and pollen evidence are lacking for the majority of disjunct or weedy species in question. Pollen assemblages are naturally biased towards species that are wind pollinated and grow in the vicinity of deposition basins, such as bogs or sediment-filled lakes. Even if conditions for deposition are favorable, the pollen of some species does not preserve well (such as *Juncus*) and identification to species or even genera can be difficult in some taxonomic groups, such as Poaceae and Chenopodiaceae. Care must also be taken to ensure that modern pollen has not contaminated the sample. Macrofossils (including preserved leaves, twigs, or floral parts) typically have a much better taxonomic resolution, but are also rarely preserved, with

the exception of bog or lake habitats and packrat middens. Of course the absence of a species from the fossil record cannot be taken as proof that it was not present.

Despite these limitations, fossils have provided evidence that several commonly presumed non-native species were, in fact, present in parts of North America prior to Columbus. Whether these native weeds subsequently spread to new parts of the continent following the expansion of European culture is a separate question that is not as easily resolved.

For nearly a century, monographers considered the North American species in the genus *Corispermum* to be conspecific with Eurasian taxa based on their morphologic similarity and propensity for weedy, disturbed habitats. Species of *Corispermum* are commonly called bugseeds due to their relatively large, flattened, and often membranous-margined fruits that superficially resemble a squashed bug. Bugseed fruits are distinctive and easy to identify. Betancourt et al. (1981) discovered fossilized seeds of *Corispermum* from soil samples in Alaska, Yukon, and the American southwest and dated them using tandem accelerator mass spectrometry at ages between 4000 (New Mexico) and 38,000 years (Alaska), providing firm evidence that at least some bugseed species were present in North America well before European settlement. Mosyakin (1995) re-assessed the taxonomy of the group and found subtle, but consistent morphological characters to recognize at least nine native North American taxa. One of the new species, *C. navicula*, is a narrow endemic of sand dunes in North Park, Colorado and might reasonably be considered a species of conservation concern. Two other Eurasian species (*C. hyssopifolium* and *C. nitidum*) are still thought to be introduced in North America, but neither is apparently well established. It should be noted that Thomas Nuttall, author of the premier early 19th century flora of North America, considered at least one bugseed, *C. americanum,* to be native.

Common purslane (*Portulaca oleracea*) is one of the world's most widespread and abundant weedy species. Traditionally, it has been considered native to India or Saharan Africa but introduced elsewhere. The species has been known in North America since Columbus documented it in Cuba and early 19th century explorers found it in Missouri and Colorado (Williams 2003). Recently, pollen and seed identifiable as *P. oleracea* have been found at archaeological sites in Kentucky, Louisiana, and Ontario that date from 600-3000 years ago. At Crawford Lake in Ontario, purslane pollen and seed can be dated in annual lake sediments to 1430-1489 AD and are found in association with maize, sunflowers, and cultivated bean fossils, suggesting that purslane may have been a food source for native peoples. Both the seeds and leaves of purslane are edible and have the highest amounts of omega-3 fatty acids and antioxidants of any plants that have been tested.

Carpetweed (*Mollugo verticillata*) is often considered native to the New World tropics, though herbarium collections place it in Ohio as early as 1828. Chapman et al. (1974) report seeds of carpetweed from an archaeological site at Icehouse Bottom, Tennessee dating to approximately 1170 years ago. Additional pre-Columbian carpetweed fossils are known from Louisiana and Alabama (Byrne and McAndrews 1975). Although related species of carpetweeds are edible, *M. verticillata* is not widely used and probably grew as a "weed" in disturbed soil of Native American garden plots.

The common reed (*Phragmites australis*) is an aggressive invader of wetland sites. Genetic evidence suggests that there are both native and non-native genotypes of the species in North America (Saltonstall 2002). Hansen (1978) discovered macrofossil remains of *P. australis* from giant ground sloth coprolites (fossil poop) in the Grand Canyon of Arizona that date to 40,000 years ago. Macrofossil remains of *Phragmites* rhizomes have also been discovered from tidal wetlands of Connecticut and the North Atlantic Coast that are 2000-4000 years old. Although present in pre-Columbian times, fossil evidence suggests that *P. australis* was a minor component of coastal wetlands until relatively modern times.

Many other weedy native species appear in pre-European fossil sites in North America and provide evidence for Native American agricultural and land-disturbance activities (Jackson 1997). Such species include ragweeds (*Ambrosia* spp.), beeplants (*Cleome* or *Peritoma* spp.), spurges (*Euphorbia* and *Chamaesyce* spp.), globe-mallows (*Sphaeralcea* spp.), and tidestromia (*Tidestromia* spp.). These species are generally not considered adventive in North America because they are not found outside of the continent, or have only invaded other areas in recent years.

Fossil data have also been used to date the first appearance and subsequent spread of non-native species that invaded North America following European contact. Pollen samples from Crawford Lake show that *Rumex* and *Plantago* pollen (ostensibly representing *R. acetosella*. *P. lanceolata*, and *P. major*) first appear in the early 1820s, coinciding with the establishment of European agriculture in southern Canada (McAndrews 1988). Pollen samples from other locations in North America show that Russian-thistle (*Salsola* spp.), hemp (*Cannabis sativa*), hops (*Humulus lupulus*), alfilaria (*Erodium cicutarium*), purple loosestrife (*Lythrum salicaria*), and various cereal grasses appeared or became abundant only following white settlement.

Historical Data

Webb (1985) notes that historical records can show when a species was first recorded in an area, but cannot prove nativity. Evidence from ship manifests, seed catalogues, and published reports can corroborate the introduction of most crop and ornamental species to North America (Mack 1990). Problems remain proving the nativity of disjunct or wide-ranging weedy spe-

cies, though early herbarium specimens, naturalist notebooks, or published reports can at least provide a first date of appearance. Combined with other evidence, historical data can make a persuasive argument for potential nativity.

Blowout penstemon (*Penstemon haydenii*) is a native species long thought to be endemic to the Nebraska Sand Hills. In 1996, BLM range ecologist Frank Blomquist discovered a small population of blowout penstemon in high, shifting sand dunes at the west end of the Seminoe Mountains in Carbon County, Wyoming, approximately 300 km west of the nearest known population in Nebraska. Immediately after this discovery, a prominent researcher in Nebraska questioned whether the Wyoming occurrence was native or possibly introduced from seed he supplied to an unspecified Wyoming gardener in the early 1980s. To complicate matters, blowout penstemon is listed as Endangered under the US Endangered Species Act. Legal protection under the Act would be limited only to the Nebraska populations if the Wyoming plants were found to be introduced.

Fortunately, historical data from herbarium specimens and 19th century government research reports have helped shed light on this case. In his original description of the species, Watson (1891) reported *P. haydenii* in Wyoming based on a specimen collected by Ferdinand Hayden from "the Laramie Mountains" deposited at Harvard's Gray Herbarium. Unfortunately, Hayden did not include a collection number or date on the specimen label. Francis Pennell believed this specimen was a duplicate of another unnumbered and undated Hayden collection of *P. haydenii* labeled "Loup Fork" collected during an 1857 expedition in the Nebraska Sand Hills and deposited at the Missouri Botanical Garden. Hayden and his team of surveyors and geologists were in Wyoming in August 1877 and crossed Sandy Creek Pass along the west side of the Seminoe Mountains on the 28th while traveling between Rawlins and Casper. Hayden notes in his *Eleventh Annual Report* of 1879 that they found dunes where "… fine sand is blown up upon the hillsides for a distance of 500 to 600 feet". The only dunes fitting this description are the ones between the Seminoe and Ferris Mountains, where *P. haydenii* has been found in recent surveys. Thus, Hayden's collections of his namesake plant were probably taken in both Wyoming and Nebraska, with Pennell having mistakenly presumed the Wyoming reports were in error (Fertig 2001).

Western larch (*Larix occidentalis*) is a native species of northwestern North America that was discovered growing on the west side of the Teton Range in Wyoming in the early 1980s. Hartman et al. (1985) reported that the stand of mature trees, located outside a popular campground, were apparently native due to their size and maturity. It was later determined from local historians that the trees were actually planted in the 1930s by the Civilian Conservation Corps, and were thus not native to the area.

*Below: Russian-thistle (*Salsola tragus*) is not a true thistle (*Cirsium*), but did arrive in North America from Eurasia. Once here, it hybridized with other* Salsola *taxa to form a new North American form in California,* S. ryanii. *Does this make* S. ryanii *native to California? Photo by Al Schneider (www.swcoloradowildflowers.com).*

Location data from type specimens can help inform whether a species should be considered native. Pineapple weed (*Matricaria matricarioides*) occurs in disturbed habitats over much of North America and is cited as non-native in most eastern floras. The earliest specimens of this plant were taken by Lewis and Clark in June 1806 "along the banks of the Kooskoosky" in Clearwater County, Idaho (Phillips 2003), suggesting it is native at least west of the Rocky Mountains. Other weedy species considered native to western North America but adventive elsewhere include prostrate pigweed (*Amaranthus blitoides*) with a type from Iowa, windmill grass (*Chloris verticillata*) first collected by Nuttall from Arkansas, and blackcreeper sedge (*Carex phaeocephala*) with a type from San Diego, California.

There are important exceptions to the rule that type localities infer local nativity. Aven Nelson described *Salsola pestifer* from western North America under the mistaken assumption that the Linnaean name *S. tragus* was misapplied. *Salsola pestifer* is now considered synonymous with *S. tragus* and accepted as adventive from southern Europe. Other *Salsola* taxa have been described from North America, including the recently named *S. ryanii* from California, which is believed to be a recently derived fertile hybrid between *S. tragus* and *S. australis* (Hrusa and Gaskin 2008). Whether *S. ryanii* should be considered native presents an interesting conundrum.

At least one putative native species has a foreign type locality. Biennial wormwood (*Artemisia biennis*), a weedy forb often found in disturbed habitats, is usually regarded as native to western North

America but introduced elsewhere. Confusion over this plant's nativity stems from the type specimen being taken from a garden plant grown in New Zealand. The source of the seed for this plant is thought to have come from northwestern North America. An unusual, multi-branched form of this species does have a type from North America. It was first collected and named by Robert Dorn from Sweetwater County, Wyoming in 1980. Ironically, the Wyoming population has not been relocated since (and the type locality significantly altered by construction of a power plant), but the variety is still known from Boulder Mountain in southern Utah. There is a possibility that the Wyoming population was established naturally by long-distance dispersal from Utah or through human facilitation but failed to persist due to the marked differences in habitat (Fertig 2008).

Habitat

Webb (1985) notes that non-native plants tend to grow in human-influenced habitats (including cultivated gardens, agricultural fields, and disturbed sites), while native species are more likely to occupy "natural" habitats that are not dominated by humans. Some introduced crop and ornamental species, such as hollyhock (*Alcea rosea*), asparagus (*Asparagus officinalis*), and white poplar (*Populus alba*) have barely escaped from cultivation, and tend to occur only in disturbed sites near human dwellings. Many others have naturalized and can spread into both disturbed and relatively pristine sites. Examples of this latter group include some of our more pernicious weed species, like cheatgrass (*Bromus tectorum*), saltcedar (*Tamarix chinensis*), and spotted knapweed (*Centaurea maculosa*), as well as widespread species such as Kentucky bluegrass (*Poa pratensis*), redtop (*Agrostis stolonifera*), and red clover (*Trifolium pratense*) that have essentially become integrated into natural systems and are not considered noxious.

Several groups of native plant species can be confused with non-native species if assessed only on their habitat preferences. Many native "weeds" were originally adapted to disturbed sites such as buffalo wallows, landslides, burned areas, shifting river courses, and other early seral habitats and have prospered over the last three centuries following European colonization. Such species have been called "expansive" by Pysek et al. (2004) to differentiate them from non-indigenous invaders. Fossil evidence can corroborate the post-contact expansion or increase in abundance of such native weeds as ragweeds (*Ambrosia* spp.) or marsh-elder (*Iva xanthifolia*) (McAndrews 1988). Other common expansive species include small-flowered butterfly-plant (*Gaura parviflora*), leathery knotweed (*Polygonum achoreum*), buffalo-bur (*Solanum rostratum*) and cut-leaf nightshade (*S. triflorum*).

One species commonly presumed to be non-native is garden sorrel (*Rumex acetosa*) based on its long history of use as an edible species and its typical distribution in weedy sites in North America and its native Europe. In the northern Rocky Mountains, however, *R. acetosa* is found in "natural" habitats such as alpine and subalpine meadows, fellfields, and coniferous forests. This habitat preference has led some researchers to question whether these populations might not actually be native. Mosyakin (2005) presents morphological evidence that the high elevation material from North America should be recognized as a distinct, native species called *R. lapponicus*.

Native disjunct species that occupy early successional or ephemeral wetland habitats are also frequently mistaken for non-native species. One such species is mossgrass (*Coleanthus subtilis*), an inconspicuous, annual of vernal wetlands and gravel bars at scattered locations in central Europe, northern Asia, and northwestern North America. The first record of this species in North America was made on an island in the Columbia River of Oregon in 1880, prompting some authorities to consider it introduced. Mossgrass has since been documented from scattered sites in Washington, southern British Columbia, and most recently in the Northwest Territories. All populations have been associated with ephemeral wetlands, islands, or shorelines with fluctuating water levels. Catling (2009) argues that the species should be considered a rare native because of its restriction to unusual natural habitats shared by other rare species, such as the Columbia River endemic Columbian yellowcress (*Rorippa columbiae*).

Geographic Distribution

Plant species with localized ranges (endemics) or widespread and continuous distributions may be invasive or expansive at the leading margins of their range, but are generally not considered introduced unless they somehow jump a large geographic barrier, i.e. exhibit a significant disjunction. Range disjunction is a relatively uncommon phenomenon in most floristic regions. Globally, Thorne (1972) estimated the percentage of disjunct species in a typical flora to be about 1% (by comparison, about 2% of the flora of Utah consists of disjunct taxa and just 4% of the flora of Wyoming).

Several case studies have already been discussed that illustrate the difficulties in differentiating between naturally occurring disjunctions (arising by vicariance or long-distance dispersal) and those that are human-mediated. Disjunct species frequently co-occur in similar habitats or geographic areas, suggesting that such patterns represent natural phenomena. An unusually high concentration of disjunct species from the taiga and deciduous forests of northern Canada and eastern North America occur together in the Black Hills of Wyoming and South Dakota. Thermal wetlands in Yellowstone National Park support a small suite of disjuncts from comparable areas of Kamchatka (*Agrostis pauzhetica*) and the New World tropics (*Myriophyllum quitense*) (Couch and Nelson 1988; Tercek et al. 2003).

Frequency of Known Naturalization

Species that have been introduced in one area of the world may be prone to invasion in other geographic locations of similar climate. This can be a useful clue to demonstrate non-native status. For example, dozens of introduced, noxious weed species in North America have also become successfully established and troublesome in temperate areas of southern Africa and Australia, including Canada thistle (*Cirsium arvense*, ironically called Californian thistle in Australia), bull thistle (*C. vulgare*), Scotch thistle (*Onopordum acanthium*), tree-of-heaven (*Ailanthus alitissima*), Scotch broom (*Cytissus scoparius*), and horehound (*Marrubium vulgare*) (Parsons and Cuthbertson 2001).

Rapidity of spread can be another clue to suggest that a species has been introduced. Cheatgrass became established in British Columbia in 1889 but by the 1930s was widespread and dominant over most of western North America (Novak and Mack 2001). Russian-thistle and Halogeton (*Halogeton glomeratus*) had similarly rapid spreads across disturbed western rangelands following establishment in the 1870s and early 1900s, respectively (Young et al. 1999). More recently, bur buttercup (*Ceratocephala testiculata* or *Ranunculus testiculatus*) has marched across the southwest following an apparent first establishment near Salt Lake City in 1932 (Barkworth 1982).

Not all introduced species, however, disperse widely or rapidly. In fact, non-native species are often quite rare. For example, in Wyoming, 38% of non-native species are known from 5 or fewer extant populations and nearly 2/3 are known from less than 20 populations. "Rare" exotics can be potentially difficult to recognize if they occur in natural habitats rather than disturbed areas.

One such exotic is Pin-leaf seepweed (*Suaeda linifolia*), known from scattered locations in Wyoming, Nevada, and Utah, often in muddy riverbank habitats. This species is indigenous to central Asia where it is not considered invasive. Holmgren and Holmgren (2009) hypothesized that the plant was introduced and spread along the transcontinental railroad, though all known *S. linifolia* in the west have only been found since the mid 1980s.

Genetics and Phylogeography

Research on the degree of genetic differentiation between populations can be a useful tool to reconstruct the evolutionary history of a species (phylogeography) or infer the age and origin of disjunct occurrences. Genetic studies have been used to determine the region of origin for different genotypes of invasive weeds, such as cheatgrass. Such work can benefit resource managers searching for specific biological control species that might be most effective. Genome analysis has also shown that non-native species may hybridize outside of their natal region to create novel genotypes, as has been demonstrated with salt-cedar (*Tamarix* spp.) in western North America. As many as 12 of the 54 salt-cedar species native to Eurasia and Africa may have been imported to North America as ornamentals and for bank stabilization, but only two (*T. chinensis* and *T. ramosissima*) have become particularly invasive (Schaal et al. 2003). Apparently, these two taxa do not ordinarily cross in their native range but hybridize readily in North America. Genetic studies suggest that the hybrid is the most widespread form of salt-cedar across western North America. Whether novel taxa derived from two introduced parents should be considered "native" in their country of origin remains controversial (Webb 1985).

Saltonstall (2002) used DNA analysis to identify different genetic strains of common reed. As previously discussed, macrofossil evidence has shown that *Phragmites australis* was native to North America prior to European contact. Ecologists have debated whether the species was also secondarily introduced from Eurasia. The genetic studies confirm the presence of multiple native and non-native haplotypes in North America. Recent taxonomic work corroborates these findings and three subspecies are now recognized in the continent's flora. These findings are particularly important as the introduced form is highly invasive and has largely displaced native ssp. *americanus* over much of the eastern United States.

Genetic studies have helped resolve a long-standing controversy regarding the nativity of flaxleaf whitepuff (*Oligomeris linifolia*) in the deserts of the southwestern United States and adjacent Mexico. Although documented by Thomas Nuttall in the early 1800s near San Diego (and described by him as a distinct species), flaxleaf whitepuff has usually been considered an introduction from desert regions of North Africa and the Middle East. Recent genome analysis has shown that significant differentiation has occurred between North American and Old World populations consistent with establishment via a long-distance dispersal event during the Pleistocene, rather than following European colonization (Martin-Bravo et al. 2009). A similar pattern of disjunction has been shown with Mohave groundsel (*Senecio mohavensis*) of desert areas of North America and its close relative yellow groundsel (*S. flavus*) of the Middle East and between North American desert Indian-wheat (*Plantago insularis*) and Saharan-Arabian ovate Indian-wheat (*P. ovata*) (Coleman et al. 2001; Stebbins and Day 1967). In the case of these latter species pairs, sufficient morphologic and genetic divergence have occurred since the Pleistocene so that North American taxa are now considered separate, though sibling, species.

Reproductive Pattern

A high percentage of non-native species are annuals with ruderal life history characteristics that predispose them for successful invasion of disturbed habitats. Several non-native species also reproduce by apomixis (dandelion, *Taraxacum officinale*), asexual bulblets (bulbous bluegrass, *Poa bulbosa*), or they spread vegetatively (mossy stonecrop, *Sedum acre*). Weedy

natives, however, can also occupy the ruderal niche and reproduce by apomixis (various *Crepis* spp.), bulblets (alpine bistort, *Polygonum bistortoides*), or vegetative growth (numerous rhizomatous perennial grasses). Thus reproductive patterns by themselves cannot reliably confirm nativity.

Webb noted that some introduced species are incapable of reproduction without human assistance. An example of such a plant is maize, which occurs infrequently as a waif in roadside and agricultural settings, but does not become naturalized because it cannot successfully reseed without human intervention.

Means of Introduction

By definition, introduced species require a means of introduction to a new location. Knowledge of the means of introduction is often a matter of the historical record, and several cases were discussed previously. Additional examples include species that have escaped from gardens (Menzies' baby blue-eyes, *Nemophila menziesii,* or Missouri evening-primrose, *Oenothera macrocarpa*), plants used in highway beautification or soil stabilization (Palmer's penstemon, *Penstemon palmeri* or cultivated flax, *Linum usitatissimum*), or intentionally introduced for crops or livestock forage (smooth brome, *Bromus inermis* or nigerseed, *Guizotia abyssinica*).

Disjunctions by native species have often been confused with introductions by humans, in part due to uncertainty over mechanisms facilitating long-distance dispersal. Paleoecological evidence has long shown that plants migrated at exceedingly fast rates in response to changes in climate, despite having limited dispersability: the so-called "Reid's Paradox". Clark et al. (1998) provide theoretical and empirical evidence that such rapid migrations are possible if populations expand through jumps rather than a broad, advancing front. Such jumps are possible by the infrequent success of chance, long-distance dispersal events. Viewed in this light, disjunct distributions of large-seeded species like blowout penstemon or white spruce (*Picea glauca*) do not have to be explained by human intervention or vicariance.

*Above: Alfilaria (*Erodium cicutarium*): historical and fossil evidence provide conflicting evidence that this common weedy species might actually be native to North America. Photo by Al Schneider (www.swcolorado wildflowers.com).*

Unresolved Cases

For the vast majority of species determining nativity is simple and straight forward. In more problematic cases, researchers should follow the advice of Webb (1985), Pysek et al. (2004), and Willis and Burks (2006) and consider multiple lines of evidence to assign nativity. Authors of state or regional floras should explicitly state their assumptions to make the process of assigning native status more transparent and defensable.

Despite our best efforts, some species remain problematic. One of the best known examples is Kentucky bluegrass (*Poa pratensis* or *P. agassizensis*). Authors disagree whether populations from the Rocky Mountains and Great Plains are native (*P. agassizensis*) or introduced from Europe (*P. pratensis*). The two taxa have subtle morphological differences in leaf pubescence and the roughness of the panicle branches and are recognized as separate subspecies (under *P. pratensis*) in the recent Flora of North America treatment. Historical data place *P. pratensis* in Canada as early as 1749, where it was collected by Linnaeus' student Peter Kalm. Traditionally, Kentucky bluegrass is presumed to have been spread by early colonists along the Atlantic seaboard and the Mississippi drainage. Anecdotal evidence suggests that Native Americans had no name for the species. Fossil data have not been of help, as grass pollen and macrofossils are notoriously difficult to determine to species or genus. Genetic analysis would be useful to resolve the taxonomy and clarify phylogeography, but unfortunately have not been conducted on *P. agassizensis*. In the absence of additional data, the case remains unresolved.

I will close with one final, enigmatic case. Alfilaria or crane's-bill (*Erodium cicutarium*) has traditionally been presumed to be introduced due to its abundance in weedy, disturbed habitats and its distribution in Europe. Historical and paleobotanical evidence appear to be contradictory, however. *Erodium cicutarium*
was documented as early as 1820 by the Long expedition in Colorado, well before the area was widely settled and converted to ranching and farming (Williams 2003). Stott et al. (1998) present pollen evidence that *E. cicutarium* was present in the Santa Barbara area of California before Spanish missionaries arrived in 1769. But other pollen studies show that the species was absent in southern California before the settlement era (Cole and Wahl 1999). Could alfilaria have been present as an uncommon native weed (like purslane and carpetweed) before European contact?

Knowing whether a plant species is native or introduced is less clear-cut than it might appear. Many disciplines, ranging from paleobotany to genetics, play an important role in determining nativity. Conservationists need to get such determinations correct, lest we expend time and resources on species protection or eradication that are unwise or unnecessary.

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*Above: Chicory (*Cichorium intybus): *Historical records confirm that this coffee-substitute was intentionally introduced to North America. Photo by Al Schneider (www.swcolorado wildflowers.com).*

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Utah Botanica
Odds and Ends from Utah Botany

A New Sandwort for Utah:

In recent years taxonomists have resurrected the genus *Eremogone* for species with narrowly linear leaves and 6-toothed capsules that were formerly included in the genus *Arenaria* (sandworts) of the pink family (Caryophyllaceae). While working on their treatment of *Eremogone* for the upcoming final volume of the *Intermountain Flora*, Noel and Pat Holmgren of the New York Botanical Garden examined hundreds of specimens in the *Eremogone kingii/fendleri* complex and became convinced that collections traditionally identified as *Arenaria kingii* var. *uintahensis* were sufficiently distinct to warrant recognition as a full species. Unfortunately, the name *uintahensis* turned out to be unusable, because the type collection of the variety was actually a specimen of *A. kingii* var. *glabrescens*. With no legitimate name available, the Holmgrens were forced to come up with a new name of their own.

Enter "Arnow's sandwort" or *Eremogone loisiae*, named to commemorate longtime Garrett Herbarium curator, Lois Arnow. In addition to her work building the University of Utah's herbarium, Arnow also wrote the *Flora of the Central Wasatch Front, Utah* and resolved many taxonomic problems in the Poaceae (grass family).

Eremogone loisiae can be distinguished from *E. fendleri* by its more ovate sepals and from *E. kingii* var. *glabrescens* by its larger sepals (4-7 mm long vs. 2.2-5 mm). Arnow's sandwort is most similar to *E. eastwoodiae*, but has longer and more flexuous basal leaves (2.5-5 cm long), and larger styles and seeds. This new species is restricted to the Wasatch Range and vicinity, from southern Idaho to central Utah (Cache and Rich to Sanpete counties) and Uinta County, Wyoming.

Holmgren, N.H. and P.K. Holmgren. 2011. A new species of Eremogone (Caryophyllaceae) from northern Utah and southeastern Idaho, USA. Brittonia 63(1):1-6.

Ode to the Staminode, Part II:

In the July issue of the *Sego Lily*, Peter Lesica answered the age-old question of "What good is a sterile staminode" in the genus *Penstemon* Scrophulariaceae or Plantaginaceae*). Alert reader and retired pollination biologist Vince Tepedino noted some recent papers that shed additional light on why beardtongues have a beardtongue.

In the case of the Blowout penstemon (*P. haydenii*, also discussed on page 6 of this issue), the removal of the staminode had different effects on pollinating bees depending on their size. Larger insects, such as bumblebees (*Bombus*) and masarid wasps (*Pseudomasaris vespoides*) were completely unaffected by elimination of the staminode. The native bee *Osmia brevis*, which normally straddles the staminode to reach the pollen-bearing anthers, compensated in altered flowers by merely stretching its legs to still gain access to pollen. Only the smaller sweat bees (*Dialictus pruinosus*) were befuddled by the lack of a staminode and frequently left the flowers without picking up any pollen. Overall, fruit set and seeds per fruit differed little between *P. haydenii* flowers with or without staminodes. In those penstemon populations in which the larger pollinators were common, the staminode of *P. haydenii* is probably truly vestigial, but where small pollinators are important, the staminode is still essential for sexual reproduction (and thus evolutionarily adaptive).

Dieringer and Cabrera R. (2002) also found a link between pollinator size and staminode function in Foxglove beardtongue (*Penstemon digitalis*) of open woods and prairies of eastern North America. Removal of the bristly staminode resulted in a marked reduction in the amount of pollen deposited on the stigma by visiting bees, but did not seem to affect total pollen removal. However, the researchers found that both large and small-bodied bees removed much less pollen when the staminodes were gone, while medium-sized bees were apparently unaffected (accounting for the total amount of pollen removal appearing unaffected).

Interestingly, pioneer ecologist Frederic Clements conducted experimental work with staminode removal in the 1920s and also found that the absence of the bearded tongue affected pollinators differently depending on their size - *W. Fertig*

*I still can't get used to that change.

*Above: Blowout penstemon (*Penstemon haydenii*) from sand dunes of central Wyoming. Photo by W. Fertig.*

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