RESEARCH ARTICLE

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Rapid range expansion of a newly formed allopolyploid weed in the genus *Salsola*[1]

Shana R. Welles[2] and Norman C. Ellstrand

PREMISE OF THE STUDY: Newly formed species (neospecies) can experience a variety of demographic fates, ranging from rapid invasive expansion to rapid extinction. Here we investigate the fate of the neospecies *Salsola ryanii* 10 years after its initial discovery in the Central Valley of California, USA. This species is an allopolyploid derived via hybridization between the invasive species, *S. australis* and *S. tragus*.

METHODS: We conducted a systematic collection of *Salsola* species from 53 sites in California. Species-specific intersimple sequence repeat (ISSR) markers were used to determine the species of each individual collected. The range of *S. ryanii* identified in this study was compared to the range in 2002 to determine how the range has shifted in the decade between surveys.

KEY RESULTS: In this survey, we identified 15 sites where *S. ryanii* was present (28% of sites), a significant population number increase since 2002.

CONCLUSIONS: *Salsola ryanii* has undergone a dramatic population number expansion in the decade since it was originally documented. We are not aware of any plant neospecies whose range spontaneously experienced such a dramatic expansion. *Salsola ryanii* has every indication of being just as invasive as its highly invasive parents.

KEY WORDS hybridization; invasiveness; polyploidy; hybridization; neospecies; range expansion; *Salsola*

The fate of newly formed species (neospecies) after one or several generations can vary dramatically. At one extreme (probably most common), a new species rapidly goes extinct; at the other extreme, the neospecies establishes itself, rapidly expands its range, and becomes a dominant species (Levin, 2000). Ascertaining how the range of a neospecies changes through time is important in order to determine both its long-term sustainability and the likelihood of whether the neospecies is likely to become invasive (Sakai et al., 2001; Neubert and Parker, 2004).

The fate of new species is typically difficult to document. Most new species evolve via incremental changes, creating a continuum between the progenitor species and the neospecies, making it difficult to characterize the early range dynamics. In contrast, new species that arise via quantum speciation involve a genetically discrete speciation event (Scudder, 1974). To illustrate, a new species that evolves via polyploidy can easily be distinguished by an increase of chromosome number relative to its ancestors, which causes the neospecies to be reproductively isolated from its progenitor species (Grant, 1981). Because of the unique characteristics associated with polyploid speciation, these species provide unique opportunities to study early range dynamics as well as to better understand polyploidy and hybridization as evolutionary forces.

Given that polyploidy may cause rapid speciation, it is not surprising that the few studies documenting the spread of newly formed species usually involve cases of allopolyploid speciation (Novak, Soltis, and Soltis, 1991; Raybould et al., 1991; Ingram and Noltie, 1995). Perhaps the best-known case involves two New World allopolyploid species of *Tragopogon*—*T. mirus* and *T. miscellus*—which evolved via hybridization followed by whole genome duplication (polyploidy) between introduced diploid Old World species (Ownbey, 1950). The first surveys identified one population of *T. mirus* and two populations of *T. miscellus*. Thirteen years later, follow-up surveys found that both species had experienced modest range expansions (to four and three populations, respectively) (Brehm and Ownbey, 1965). Further work showed continued range expansion such that by 1990, *T. mirus* was present in 10 populations and *T. miscellus* in 38 (Novak, Soltis, and Soltis, 1991).

In addition to facilitating speciation, hybridization and polyploidy have both also been proposed to be important in the evolution of invasive species (Ellstrand and Schierenbeck, 2000; Schierenbeck and Ellstrand, 2009; te Beest et al., 2011; Pandit, White, and Pocock,

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Department of Botany and Plant Sciences, University of California–Riverside, Riverside, California 92521
[2] Author for correspondence: (shana.welles@e-mail.ucr.edu)
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2014). In a recent review, Schierenbeck and Ellstrand (2009) documented 24 invasive species resulting from hybridization, nine of which result from allopolyploidy. Given the documented importance of allopolyploidy in the evolution of new species and invasive species, an ideal system for investigating the early range dynamics would involve (1) an annual species that reproduces within its first year so that range changes can be measured over a reasonable time, and (2) a species that is extremely new, so that it can be "caught in the act" of early range changes.

The recently evolved *Salsola ryanii* (Amaranthaceae) fits these two qualifications. It is an annual allohexaploid ($2n = 54$) hybrid of *S. tragus* ($2n = 36$) and *S. australis* ($2n = 18$) (Hrusa and Gaskin, 2008; Ayres et al., 2009). Prior to this study, *S. ryanii* was known from three populations, all in the Central Valley of California, USA, (denoted as blue dots, Fig. 1), from two geographic regions of the California Floristic Province, as assigned by *The Jepson Manual* (Baldwin and Goldman, 2012). Two of these populations were collected in a 2002 survey, and the third was documented in 2008 (Akers et al., 2002; Hrusa and Gaskin, 2008; Ayres et al., 2009). To our knowledge, there is no documentation of *S. ryanii* prior to 2002, and no in-depth surveys of *Salsola* in California were completed prior to this time. The 2002 survey that initially documented *S. ryanii* (at the time called *S. tragus* type C) was a broad survey with the goal of documenting the species and types of *Salsola* present within California (Akers et al., 2002). This survey used a combination of isoenzyme and morphological markers, and for some individuals RAPD DNA markers to identify the individuals collected by species and type; it included 89 collection sites, most of the collections were well dispersed throughout the Central Valley of California. The survey also included two collections around the Bay Area of California and four collections in Southern California (Akers et al., 2002).

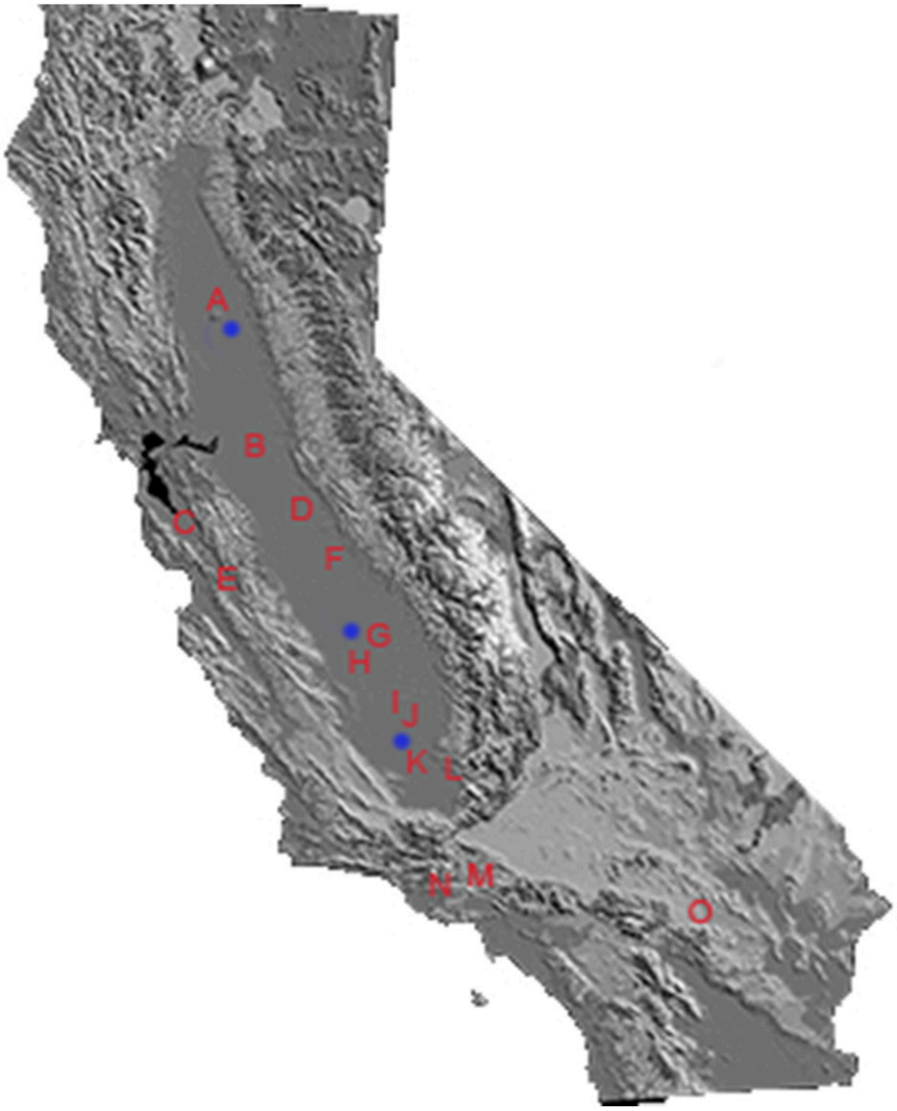

FIGURE 1 Map of *Salsola ryanii* distribution. Blue dots indicate populations that were identified in the 2002 survey conducted by Akers et al. (2002) or by Ayres et al. (2009). Red letters indicate newly identified populations in this study. Letters correspond to letters in Table 1 where additional information is presented on the makeup of the population.

Salsola ryanii evolved via hybridization between two problematic invasive species, therefore it is important to determine whether this neospecies has potential to become invasive (Akers et al., 2002; Hrusa and Gaskin, 2008). Prior to this study, it was unknown whether *S. ryanii* had expanded from the three previously known populations or whether it had the potential to become invasive (Hrusa and Gaskin, 2008; Ayres et al., 2009). Hrusa and Gaskin (2008) predicted that *S. ryanii*'s ecological intermediacy would prevent it from drastically expanding its range or becoming invasive. In this study, we conducted a large survey of *S. ryanii* to determine how the range has shifted in the decade following initial detection; understanding how the range has shifted will further our understanding of the potential invasiveness of this neospecies.

MATERIALS AND METHODS

Study species—*Salsola ryanii* is an allopolyploid species formed via hybridization and whole genome duplication between *S. tragus* and *S. australis*. Neither progenitor species of *S. ryanii* is native to California. *Salsola tragus*' native range extends from North Africa and Western Russia, through Asia into Northeast Siberia and Northeast China. The first known introduction of *S. tragus* into North America occurred in South Dakota in the 1870s, likely through contamination of agricultural seed (Young, 1988). The number of introductions of *S. tragus* into the USA is unknown, but the introduction source was likely Russia (Young, 1988). *Salsola tragus* has a $2n$ chromosome number of 36, compared to a base chromosome number for the genus of $2n = 18$, suggesting that *S. tragus* is of tetraploid origin (Ayres et al., 2009). *Salsola australis* is a weed that is invasive in California and Arizona, and is likely native to Australia or South Africa

(Borger et al., 2008). *Salsola australis* is morphologically very similar to *S. tragus* and was not recognized as a distinct species until recently (Ryan and Ayres, 2000). Given that *S. australis* was an unrecognized cryptic species assigned to *S. tragus* until recently, it is not known exactly when *S. australis* was introduced into North America.

All three *Salsola* species occur on highly disturbed habitats (S. Welles, personal observation). The well-known *S. tragus* is considered a problematic weed in 48 US states (plants.usda.gov) and has been described as having the most rapid spread of any introduced species (Rilke, 1999). In this study, we broadly collected *Salsola sp.* within California to determine how the range of *S. ryanii* has shifted since the prior surveys.

Sample collection—In the summer of 2012, individuals belonging to the genus *Salsola* were systematically collected from 53 sites throughout regions of California. Collections in this study included broader sampling from the coastal range and slightly broader collecting in Southern California than the previous survey. Four collections, each a minimum of 10 miles apart from each other, were sampled from each of 26 square quadrats throughout the state (unless four populations that were an adequate distance apart could not be located), for a total of 53 collections. Each collection contained up to 20 individuals. Note that for many of the coastal quadrats, less than four collections were made per quadrat because of the lack of available populations. Plants of different sizes were intentionally sampled. Locations of all collections were tracked using a Garmin GPSmap 62s unit.

Sample identification—Following collection, up to 0.4 g of vegetative tissue from each sample was cut and frozen. DNA was extracted from all samples using a modified CTAB procedure (Ryan and Ayres, 2000). DNA was quantified using a nanodrop-1000. All samples were diluted to 50 ng/µl. Intersimple sequence repeats (ISSR) markers were used to genotype individuals using primers 810, 835, 840, and 890, as described in Ayres et al. (2009). Species-specific bands for *S. australis* and *S. tragus* were scored as either present or absent. Individuals with all species-specific bands belonging to both of the parental species were determined to be the allopolyploid species (S. *ryanii*) as described by Ayres et al. (2009). This method provides a conservative identification tool; because an individual must have all progenitor bands to be classified as hybrid, any misidentified individuals are likely to be hybrids misclassified as one of the progenitor species, as opposed to one of the progenitors misclassified as hybrid.

Using ISSR markers to identify the species of each sample, it is difficult to distinguish homoploid from polyploid hybrids. Given the difference in chromosome numbers between the two progenitor species, homoploid hybrids would have problems in meiosis and would be sterile (Grant, 1981). Therefore, any plant that is determined to be of hybrid origin via ISSR markers and has viable seed is an allopolyploid as opposed to a homoploid hybrid. For this reason, we resampled from each of the sites where hybrids were identified and we revisited during fruiting to confirm that the hybrids that were identified were the allohexaploid species *S. ryanii* and not homoploid hybrids.

To test whether the range has significantly changed between the two surveys, we used a Fisher's exact test done in R (R Core Development Team, 2014). Only *S. ryanii* populations within the Central Valley of California and Southern California were included in the analysis because these were the areas that were sampled the most thoroughly in the previous survey.

RESULTS

Of the 53 collections that were made in this study, 15 contained *S. ryanii* (Table 1), 21 contained *S. tragus*, and 26 contained *S. australis*; some populations included multiple species. Of the 15 collections that contained *S. ryanii*, four contained only individuals identified as *S. ryanii;* all other *S. ryanii* populations also included one or both of the progenitor species. We were able to resample 12 of these populations the following year; in the other three sites, it appeared that weed control methods, such as tilling and herbicides, had been used to eliminate all *Salsola*. Seeds from all collected plants identified as hybrid germinated, indicating that they are allopolyploid *S. ryanii*, because homoploid hybrid plants would not produce viable seed.

TABLE 1. Location and species makeup of collections that include *S. ryanii*. Map ID letters correspond to letters on Fig. 1 representing collection locations. Percentages represent the species identification for all individuals identified from that particular collection. Only collections which contain *S. ryanii* are presented here.

Map ID	% *S. ryanii*	% *S.tragus*	% *S. australis*	Individuals collected	Seeds recollected	California floristic province region[1]	GPS Coordinates
A	100	0	0	14	Yes	Sacramento Valley	39°00.368′N 121°4.022′W
B	33	66	0	14	Yes	San Joaquin Valley	38°11.531′N 121°39.420′W
C	100	0	0	10	Yes	San Francisco Bay Area	37°21.829′N 121°74.175′W
D	93	7	0	15	Yes	San Joaquin Valley	37°30.400′N 120°50.417′W
E	8	83	8	11	Yes	San Francisco Bay Area	36°99.548′N 121°56.318′W
F	100	0	0	19	No	San Joaquin Valley	36°99515′N 120°10.641′W
G	75	0	25	16	Yes	San Joaquin Valley	36°73.878′N 119°89.739′W
H	100	0	0	9	Yes	San Joaquin Valley	35°60.028′N 119°89.739′W
I	50	0	50	6	Yes	San Joaquin Valley	36°05.341′N 120°06.976′W
J	87	0	13	15	Yes	San Joaquin Valley	35°43.921′N 119°44.583′W
K	25	50	25	6	Yes	San Joaquin Valley	35°36.466′N 119°34.817′W
L	60	40	0	15	No	Tehachapi Mountain Area	35°07.582′N 118°24.865′W
M	30	0	70	10	Yes	Western Traverse Ranges	34°30.733′N 118°32.070′W
N	50	0	50	20	Yes	Central Coast	34°34.464′N 119°07.656′W
0	89	0	11	9	No	Modoc Plateau	33°42.463′N 116°14.949′W

[1] Geographic regions of the California Floristic Province (Baldwin and Goldman, 2012).

The Fisher's exact test comparing the number of Central Valley and Southern California populations in the current survey (12 populations) compared to the 2002 survey conducted by Akers et al. (2002) (2 populations) demonstrates the current population number is significantly larger than the previous survey ($P < 0.0001$). If we include only Central Valley populations, which both surveys sampled thoroughly (current survey—nine *S. ryanii* populations, 2002 survey—two *S. ryanii* populations) a Fisher's exact test demonstrates the number of populations in the Central Valley is significantly larger currently compared to 2002 ($P = 0.003$).

In addition to a significant expansion of *S. ryanii* in the Central Valley, in this survey we also identified populations of *S. ryanii* in Southern California and more coastal regions of Northern California (Fig. 1, Table 1). We cannot be certain when the coastal populations appeared because of the minimal sampling of these areas in the earlier survey.

Populations of *S. ryanii* that had previously been mapped were present in two geographic regions of the California Floristic Province (Baldwin and Goldman, 2012): the Sacramento Valley region and the San Joaquin Valley region. Collections identified as *S. ryanii* in the current study were located in six different geographic regions: the two geographic regions where the previous collections were made and four geographic regions where *S. ryanii* had not previously been documented (see Table 1). Of the 15 populations of *S. ryanii* that were identified in this survey, 11 populations were within the range that was sampled sufficiently in the previous study. The other four populations are in a region that included minimal sampling.

DISCUSSION

In a single decade, *Salsola ryanii* has rapidly and dramatically expanded the number of populations within the area where it was originally documented and expanded its range into Southern California. In this survey, we also documented the presence of *S. ryanii* on the coast of California, however we cannot determine that this expansion occurred within the last decade because the sampling in this region in the previous survey was limited to two collections.

To our knowledge, this is the fastest documented population number expansion of a newly formed allopolyploid species—perhaps the most dramatic known range expansion of any plant neospecies. Previous studies demonstrated that multiple morphological characters of *S. ryanii*'s are intermediate between its progenitors; specifically, fruit wing size, timing of fruit maturity, fruit position on stem, fruit persistence on plant, and tumbling dispersal behavior (Hrusa and Gaskin, 2008). Hrusa and Gaskin (2008) predicted that the intermediate morphology of *S. ryanii* would prevent it from being as well adapted as either of its progenitor species, and would greatly limit potential range expansion, preventing *S. ryanii* from becoming a widespread weed (Hrusa and Gaskin, 2008). The range expansion documented in this study contradicts the prediction that *S. ryanii*'s success as weed would be limited by its intermediate morphology compared to its progenitors.

This population number expansion could be occurring via two possible nonmutually exclusive mechanisms: (1) propagule dispersal, or (2) multiple independent evolutionary origins. The data presented here do not allow us to determine which of these mechanisms are responsible for the range expansion documented in this study. Hrusa and Gaskin (2008) suggested that each of the three originally documented populations were likely the result of independent origin events due to the disjunct nature of the populations, however, this needs to be confirmed using molecular methods. The *Salsola* genus is documented to have high levels of dispersal (Mitchell and Wilcox, 1988). The parents vary in their dispersal; *S. tragus* exhibits the "tumbling" dispersal that is characteristic of the genus, which allows for very long range dispersal, while *S. australis* is also highly dispersed via wind but does not "tumble" (Mitchell and Wilcox, 1988; Borger et al., 2008). The dispersal mode in *S. ryanii* has not been studied, but the similarities between the progenitors and the neospecies suggest that *S. ryanii* is also highly dispersed. Because of the evidence for multiple origins and the high level of dispersal in this group, it seems likely that the population expansion documented in this study involves both propagule dispersal and repeated de novo formation of hybrid populations via polyploidy in areas where the two progenitor species have colonized.

Salsola ryanii's dramatic population number increase (an expansion of one population per year) within a decade is in stark contrast to other previously documented range expansions in allopolyploid neospecies. The two neopolyploid North American *Tragopogon* species represent the very best studied examples. The more rapidly expanding of the two, *T. mirus*, expanded from one to three locations in the first 13 years following initial documentation (expansion of 0.31 populations per year) (Brehm and Ownbey, 1965). We can also compare the range expansion of *S. ryanii* to the well-studied neoallopolyploid, *Senecio cambrensis*, derived via hybridization between *S. squalidus* and *S. vulgaris* (Ashton and Abbott, 1992). *Senecio cambrensis* has evolved twice, independently in the United Kingdom—both in Wales and Edinburgh, Scotland (Ashton and Abbott, 1992; Harris and Ingram, 1992). The Welsh origin experienced modest range expansion from 1–10 populations between initial discovery in 1950, and follow-up surveys in 1995 (expansion of 0.005 populations per year). In contrast, within 10 years after its initial discovery, the Edinburgh population was extinct (Ingram and Noltie, 1995; Abbott and Forbes, 2002).

Allopolyploidy has long been recognized as important to the origin of new species and a major evolutionary mechanism in most major plant groups (Grant, 1981; Wood et al., 2009; Jiao et al., 2011). Despite the frequency of polyploidy in plant evolution, current evidence fails to support any special evolutionary advantage to polyploid lineages and suggests that they have a relatively low diversification rate (Mayrose et al., 2011). The rapid spread of *S. ryanii*, provides evidence that allopolyploidy can produce species that are able to quickly spread following initial formation.

In comparison with other well-studied cases of range expansion of neospecies, it is clear that *S. ryanii* represents an extreme example. Given this population number expansion in just a decade, it seems likely that the range of *S. ryanii* will continue to expand and is likely to become an important invasive species. These results strongly contradict the predictions in early studies of *S. ryanii* that it would not likely become invasive (Hrusa and Gaskin, 2008). Given the dramatic range increase that has been documented in California, it is also possible that *S. ryanii* could become an invasive species in other countries through either dispersal of seed of *S. ryanii* from California or through recurrent formation in other locations where progenitor species co-occur.

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