Evolution of increased vigour associated with allopolyploidization in the newly formed invasive species *Salsola ryanii*

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Abstract

A correlation between allopolyploidization and increased fitness is an explanation for the importance of allopolyploidy throughout evolution, specifically plant evolution. Although many authors have suggested correlation between allopolyploidy and increased fitness, common garden comparisons testing hypotheses about fitness shifts associated with allopolyploidy are lacking. In this study, we test the theory that allopolyploidy is associated with increased fitness in the newly formed allopolyploid weed *Salsola ryanii*. We conducted a common garden comparison over 2 years to determine how different fitness correlates (plant volume, plant mass and estimated seed number) of the newly formed allopolyploid species *S. ryanii* compares to its progenitors (*S. tragus* and *S. australis*) at a site within the range of all the newly formed allopolyploid and both of its progenitors. We document an increase in above-ground plant mass and above-ground volume in the newly formed allopolyploid compared to its progenitors. Plant mass and volume of the newly formed allopolyploid relative to its progenitors was dependent on year. The results of this study support the hypothesis that allopolyploidization is associated with increased growth, which is consistent with predictions that allopolyploid lineages experience vigour due to fixed heterozygosity.

Keywords: Common garden; fitness; hybridization; polyploid.

Introduction

Ploidy (whole-genome duplication) is the most important cytogenetic mechanism in plant evolution (Otto and Whitton 2000; Solis et al. 2009; Madlung 2013; Wendel 2015). Angiosperms and most other land plants have an evolutionary history that includes multiple polyploidization events (Wendel 2000, 2015; Jiao et al. 2011; McGrath and Lynch 2012).

Allopolyploidy (hybridization fixed by whole-genome duplication) is either considered to be the primary source of successful polyploid lineages (Scarpino et al. 2014) or is at least co-equal to autopolyploidy (Barker et al. 2016). The establishment of an allopolyploid neospecies begins with a few individuals of the nascent species at a very low frequency relative to their progenitors. If their fitness is inferior relative to the parental types, the new lineage should go extinct promptly. If their fitness is roughly equal to that of their parents, they might persist longer, but their chance of long-term persistence in the face of demographic stochasticity is quite low (Fowler and Levin 2016). Given the abundance of species identified as allopolyploid, an immediate fitness advantage relative to the parental taxa might be presumed.

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Early studies hypothesized that increased fitness or ecological success of allopolyploid lineages is associated with fixed heterozygosity (Stebbins 1947, 1950). It was also been proposed that long-term evolutionary success in allopolyploid species may also be associated with increased ability to adapt to novel or disturbed habitats (Ehrendorfer 1980; Lewis 1980; Levin 1983). Both polyploidy and hybridization have also been proposed as pathways to the evolution of invasiveness (Stebbins 1970; Abbott 1992; Ellstrand and Schierenbeck 2000; Pandit et al. 2006, 2011). Interestingly, the relevant fitness data to determine how the fitness of allopolyploid lineages compares with their progenitors is lacking. A few descriptive studies have suggested that allopolyploids are competitively superior to their parents (e.g., Arrigo et al. 2016). We are not aware of an experimental study that has compared fitness or fitness correlates between allopolyploid lineages with their progenitors.

Early studies of plant evolution by allopolyploidy hypothesized that increased fitness or ecological success, as well as increased ability to adapt to novel or disturbed habitats, was would be associated with allopolyploidization (Stebbins 1947, 1950; Ehrendorfer 1980; Lewis 1980; Levin 1983). Based on similar arguments, both polyploidy and hybridization have been proposed as a pathways to the evolution of invasiveness (Abbott 1992; Ellstrand and Schierenbeck 2000; Pandit et al. 2006, 2011). In the California flora, after accounting for life history differences between annual and polyploid species, polyploidy was found to be significantly more common amongst weeds than it is in families overall (Heiser and Whitaker 1948). There are also numerous cases in which multiple cytotypes exist within the native range of a species, but only the polyploid variants have become invasive (i.e., Centaurea maculosa, Solidago gigantea) (Treier et al. 2009; Schlaepfer et al. 2010). Furthermore, several floristic surveys identify an association between polyploidy and biological invasion (Stebbins and Major 1965; Pandit et al. 2006, 2011; Pyšek et al. 2009).

Autopolyploidy (whole-genome duplication not co-occurring with hybridization) is also associated with increased fitness and ecological success (Stebbins 1947; Ehrendorfer 1980; Lewis 1980; Levin 1983; Wei et al. 2019). Common garden comparisons between polyploid species and their diploid progenitors have also established that polyploid derivatives generally have increased plant size (Schnitzler and Muller 1998; Schlaepfer et al. 2010; Wei et al. 2019), increased flower size (Garbutt and Bazzaz 1983) and increased seed production (Bretagnolle et al. 1995) relative to their progenitors.

Multiple studies have also compared the fitness of hybrid lineages with their progenitors. Hybrid fitness can range greatly from sterile to highly successful lineages with increased fitness compared to their progenitors, sometimes evolving into a niche independent from that of their progenitor (Rieseberg et al. 2003). The phenotypes of hybrid lineages relative to their ancestors also range from intermediate to transgressive or novel phenotypes (Rieseberg et al. 2003; Gallego-Tévar et al. 2018). Processes associated with hybridization (novel gene combinations and/or expression, increased genetic variation, fixed heterosis and dumping of genetic load) are associated with increased fitness and novel or transgressive phenotypes (Grant 1981).

In addition to fitness, establishment of new cytotypes may also be limited by availability of appropriate pollen. When a new cytotype emerges in a population, the majority of the pollen that its flowers receive will be from the majority cytotype, limiting reproductive success of new cytotypes. This process is known as minority cytotype exclusion, and predicts that unless there is an ecological niche separation one of the less frequent cytotype will go extinct (Levin 1975). Multiple cytotypes have been documented to coexist in species that reproduce asexually (apomixes) (Kao 2007). Support for the minority cytotype exclusion principal is mixed (Husband 2000; Baack 2005; Sabara et al. 2013). Although theory suggests that cytotypes should be geographically assorted, mixed cytotype populations have also been documented in sexually reproducing populations. For example, in Epilobium angustifolium (Onagraceae) 60 % of populations are mixed ploidy (Sabara et al. 2013) while 69 % of populations of Galax urceolata (Diapensiaceae) (Burton and Husband 1999).

For an allopolyploid neospecies to established in the presence of its progenitors it must have an advantage that allows the neospecies to overcome the initial demographic stochasticity (Fowler and Levin 2016). In this study, we compare multiple correlates of fitness (plant mass, plant volume and seed number) between an allopolyploid neospecies (Salsola ryanii) and its progenitors (S. tragus and S. australis).

Salsola ryanii, a recently formed allopolyploid species, provides an ideal system to investigate the effects of allopolyploidy on fitness. Salsola ryanii is an annual species that has evolved within the last 25–100 years via hybridization between two introduced species, S. tragus and S. australis, both of which are invasive in California, USA (Ayres et al. 2009). Salsola ryanii is the result of multiple origin events (Welles and Ellstrand 2016a). Its current range is likely the result of multiple origin events followed by dispersal. The formation mechanism of this species, hybridization followed by whole-genome duplication or formation of non-disjunct gametes, is unknown for this species and could potentially vary between origins. Salsola tragus is a tetraploid species (2n = 36) that is native to Russia and China; it is one of the world’s worst weeds and invasive in 48 US states (Holm 1997; Ayres et al. 2009). Salsola australis is a diploid (2n = 18) that is native to Australia and South Africa and invasive in California and Arizona (Borger et al. 2008; Ayres et al. 2009). Salsola ryanii appears to also be problematic; its reported range in California is now several times larger than when it was first identified and named about 15 years ago (Welles and Ellstrand 2016a). Salsola ryanii’s entire range is sympatric with both of its progenitors (Fig. 1); at the site level it has been documented to occur alone and with one or both of its progenitors (Welles and Ellstrand 2016a). Determining how the fitness of S. ryanii compared to invasive progenitors is important to understanding the potential impacts of S. ryanii.

The goal of this common garden study was to determine how correlates of fitness of the newly formed allopolyploid species, S. ryanii, compare to those its progenitors, S. tragus and S. australis, within a common environment in the overlapping range of all three species. We hypothesize that the allopolyploid neospecies S. ryanii will have increased vigour relative to its progenitors, and that its tetraploid progenitor (S. tragus) will have higher vigour than its diploid progenitor (S. australis).

Materials and Methods

Fitness comparisons between the newly formed allopolyploid species, S. ryanii and its progenitors, S. tragus and S. australis, were completed through two common garden studies, one from 2012 to 2013 and the other from 2014 to 2015. Both studies were conducted at the Agricultural Research Station at the University of California, Riverside, in close proximity to naturalized populations of all three species. This site experiences a wide seasonality of temperatures with 100 days a year over 32 °C and an average low in the coldest month of 6 °C. Total rainfall...
in year 1 (2012–13) was 86 mm and 191 mm in year 2 (2014–15). The two common garden comparisons were conducted at different locations within the Agricultural Research Station. Both sites were tilled prior to the start of the study creating a level of disturbance similar to where all species grow. Both sites were a joining citrus tree plantings and have a history of various agricultural plantings.

**Plant material**

Plants were grown from seeds collected from throughout the Central Valley of California, USA the previous growing season. Collections ranged from Merced, CA to Bakersfield, CA and were bounded by I-5 to the West and CA-99 to the East (Fig. 1). GPS locations of sites were tracked using Garmin GPSmap 62s [see Supporting Information—Table S1](#)]. Sites where *S. ryanii* is known to be present based on surveys done by Welles and Ellstrand (2016a) were intentionally visited. *Salsola* sp. occur densely across this region of California and lack clear breaks between populations (S. Welles, pers. obs.). Collection sites were a minimum of 16 km apart. All three *Salsola* species were regularly located throughout the collection area. In the survey completed by Welles and Ellstrand (2016a) one-fourth of *S. ryanii* collections in the San Joaquin Valley were pure *S. ryanii*; however, all collection locations are in close proximity to documented occurrences of one or both progenitor species [Fig. 1]. One individual per species per collection site was planted per block. The species of each individual morphologically identified in the field based on morphological characterizations outlines by Hrusa and Gaskin (2008) and was confirmed using species specific ISSR markers following the protocol used in Welles and Ellstrand (2016a).

**Experimental design**

All seeds were germinated in flats in a temperature-controlled greenhouse, hardened in a lath house and transplanted into the field at the seedling stage in the spring, during the time seedlings typically germinate at nearby sites. Seedlings that did not survive transplantation into the field were replaced. Seedlings were watered using drip irrigation for 4 weeks to ensure successful establishment. The field was divided into three blocks. Equal numbers of each species were planted in each block with 1 m spacing between individuals. Within each block, the position of each individual was randomly determined.

The 2012–13 experiment (year 1) included a total of 119 individuals after mortality, 33 individuals of *S. tragus*, 22 individuals of *S. australis* and 64 individuals of *S. ryanii*. The 2014–15 experiment included 87 individuals following mortality, 27 individuals of *S. australis*, 23 individuals of *S. tragus* and 37 individuals of *S. ryanii*. In both experiments we estimated plant volume (width * height), and final plant mass. Mass was measured using an AWS H-110 digital hanging scale, which has a maximum capacity of 50 kg. Final height and width were measured at the widest and tallest point for each plant. Final plant width, height and wet mass were measured once fruit set was complete but prior to plant desiccation. One major branch was selected from the base of each plant in a similar location for to estimate the relationship between plant mass and fruit set. The total number of fruits present on the branch was counted and the branch was weighed.

This study included three fitness correlates; two correlates associated with plant vigour (above-ground plant biomass and above-ground plant volume) and one estimate of seed production (estimated seed number). Estimated seed numbers were calculated because counting seed numbers was time-prohibitive because all the species in this study can produce >100 000 single-seeded fruits per year. Estimated seed number is however less reliable than a full seed count, as individuals could differ in their seed density throughout the plant.

**Statistical analyses**

Analysis of variance (ANOVA) was used to analyse differences between the allopolyploid species and its progenitors in plant size, plant mass and estimated seed number calculated as whole-plant mass multiplied by subset seed count/mass of subset branch. ANOVA assumptions (heterogeneity of variance and normal distribution) were tested prior to analyses. Block was included as a random effect in the model for all analyses. All analyses were done in R version 3.3.3 (R Core Team 2014).
Results
In year 1 of the study, S. ryanii had significantly greater mass, volume and estimated seed number than its diploid progenitor (S. australis) (Tables 1 and 2). It also had greater mass and volume than its tetraploid progenitor (S. tragus), though not significantly (Table 2; Fig. 2). In year 2 S. ryanii had significantly greater mass than both of its progenitors, significantly larger volume than S. tragus and significantly higher estimated seed number than S. australis (Table 2). Which of the progenitors had greater mass and volume was dependent on the year (Table 1; Fig. 2). S. tragus had greater mass and volume in year 1 where S. australis had greater mass and volume in year 2 (Table 1; Fig. 2). The large plant size and estimated seed numbers are consistent with other studies of Salsola species, which have documented seed numbers of >100 000 seeds per plant (Young 1972, 1986).

A regression of seed number onto mass for the subset branches sampled demonstrates a strong correlation between branch mass and seed number (Pearson’s $r = 0.62; n = 86; P < 0.0001$). We do, however, also find a significant effect of species ($P = 0.0226$) in the regression analysis; S. tragus had the largest number of seeds per mass in the collected branches followed by S. ryanii and S. australis.

Discussion
In this common garden comparison, we document increases in all vigour (above-ground biomass and volume) in the allopolyploid neospecies S. ryanii relative to its progenitors. The transgressive phenotype observed for mass and volume in this allopolyploid species in year 2 of this study is consistent with common garden studies demonstrating increased size associated with autopolyploidy (Schnitzler and Muller 1998; Schlaepfer et al. 2010) and common garden studies demonstrating that certain hybrid-derived diploid lineages have increased fitness relative to their progenitors (Hegde et al. 2006). Multiple authors have provided theoretical rational for the hypothesis that allopolyploidy is commonly associated with increased fitness (Ehrendorfer 1980; Lewis 1980) and required to overcome initial demographic stochasticity (Fowler and Levin 2016); this experimental study confirms predictions that allopolyploid lineages will have high levels of vigour relative to their progenitors. The success of allopolyploid lineages has been proposed to be attributed to fixed heterozygosity, allowing for long-term retention of hybrid vigour (Grant 1981; Chen 2010, 2013). In this study, the greater increase in plant mass and volume (vigour-associated traits) following allopolyploidization is consistent with predictions that success of allopolyploid lineages is driven by heterotic effects. The magnitude of the increase in vigour is however dependent on year; plant size is increased relative to its progenitors in both years of the study; however, it is only significantly different from its tetraploid progenitor (S. tragus) in year 2, the wetter year, of our study. Salsola ryanii is more vigourous than its diploid progenitor across both years of this study.

As whole-plant fitness can be difficult to measure, multiple different fitness proxies are commonly used. While using molecular markers to determine which individuals are recruiting the most offspring is the most effective way to document fitness, plant biomass is a commonly used fitness proxy (used in 42% of studies measuring fitness) (Younginger et al. 2017). Biomass is a less reliable proxy for fitness in woody perennials (Santos-del-Blanco et al. 2013) and plants experiencing high levels of herbivory (Agrawal et al. 1999). Other than these circumstances the general rule is that larger plants of the same life stage have higher fitness (Younginger et al. 2017). An individual’s fitness encompasses survival, growth and reproduction including both female and male reproductive output as well as the success of those propagules (Primack and Kang 1989). Female fitness is linked to both number of offspring in the next generation

Table 1. Comparisons of relative size and weight between Salsola ryanii and its progenitors in a common garden study. Year 1 included 119 individuals; 64 of S. ryanii, 22 of S. australis and 33 of S. tragus. Year 2 included 87 individuals; 37 of S. ryanii, 27 of S. australis and 23 of S. tragus. Plant volume is width at the widest point squared x maximum height. Estimated seed number is based on plant mass multiplied by average number of seeds per mass in subset branch.

|          | S. ryanii (6n) | S. tragus (4n) | S. australis (2n) |
|----------|---------------|---------------|------------------|
|          | Average       | Standard deviation | Average       | Standard deviation | Average       | Standard deviation |
| Year 1   |               |               |                 |                   |               |                   |
| Mass (kg)| 1.36817       | 0.19986       | 1.24793         | 0.16444           | 0.3915        | 0.11509           |
| Plant volume (m$^3$) | 1.26964       | 1.01077       | 1.33399         | 0.75108           | 0.49222       | 0.58108           |
| Seed number | 77 306       | 210 970       | 97 329          | 50 173            | 22 121        | 22 192            |
| Year 2   |               |               |                 |                   |               |                   |
| Mass (kg)| 5.82244       | 0.77638       | 2.77923         | 0.67509           | 3.08935       | 0.84775           |
| Plant volume (m$^3$) | 2.63198       | 2.10351       | 1.34081         | 1.63533           | 1.71151       | 1.60994           |
| Seed number | 328 985      | 261 204       | 157 558         | 224 042           | 174 558       | 236 878           |

Table 2. Results of ANOVA comparing fitness correlates between the allopolyploid neospecies Salsola ryanii and its progenitors, S. tragus and S. australis. All analyses were completed in R (R Core Team 2014).

| Fitness Correlate | Factor | $R^2$ | Species | Block |
|-------------------|--------|-------|---------|-------|
| Year 1            |        |       |         |       |
| Mass (kg)         |        | 0.2202| 0.000109| 0.00235|
| Plant volume (m$^3$) |        | 0.1508| 0.00234 | 0.01765|
| Seed number       |        | 0.1736| 2.27 $\times 10^{-5}$ | 0.00326|
| Year 2            |        |       |         |       |
| Mass (kg)         |        | 0.196 | 0.00594 | 0.257 |
| Plant volume (m$^3$) |        | 0.161 | 0.00773 | 0.546 |
| Seed number       |        | 0.1684| 0.0294  | 0.26262|
coming from an individual’s seeds, which is influenced by both the number of seeds and the mass of those seeds (Lloyd 1980). The relative role of seed number and seed mass in total fitness will depend on environmental conditions and strength of competition during early life stages. While we did not measure male fitness directly in this experiment, descriptive and experimental paternity studies have demonstrated an association between plant size and male fitness (e.g. Devlin et al. 1992; Karron and Mitchell 2012; Tani et al. 2012). Absolute fitness of individual in the field will also be dependent on both the fitness correlates measured in this study combined with any fitness declines caused by flowers being pollinated with incompatible pollen (Husband 2000). Further studies should be done to determine the outcrossing rate of each species (as highly selfing species experience minimal fitness affects associated with incompatible pollen) and compare relative fruit set between single and mixed cytotype populations to determine the impact of fruit-set reductions associated with incompatible pollen as predicted by the minority cytotype exclusion theory.

This fitness comparison combined with previous work documenting S. ryanii’s ongoing rapid range expansion (Ayres et al. 2009). However, the relatively high vigour of S. ryanii compared to its progenitors demonstrates that the allopolyploid has the potential to maintain or increase its invasiveness. Salsola ryanii is a newly formed species resulting from multiple independent origin events, that have subsequently admixed (Hrusa and Gaskin 2008; Welles and Ellstrand 2016b), increasing the genetic diversity of this neospecies relative to an allopolyploid lineage resulting from a single origin event. Traits observed in this study are the result of hybridization, whole-genome duplication, followed by no >100 generations of evolution including admixture between independently formed lineages. It is possible that a species originating from a single origin or multiple independent origins that do not admix would have a different relative fitness. Future studies should investigate the relative fitness of allopolyploid neospecies resulting from both single and multiple origins to broaden our understanding of traits of allopolyploid species.

This study begins to fill the gap in our understanding of phenotypic evolution during an allopolyploid speciation event by comparing traits of a newly formed allopolyploid and its progenitor species within a common environment. Further common garden comparisons between other newly formed allopolyploid species and their progenitors are needed to establish whether the patterns observed in this system represent broad patterns associated with allopolyploid species.
Supporting Information
The following additional information is available in the online version of this article—
Table S1. Locations of Salsola seed collections used in this study.

Data
Data from this study are archived and available at https://data.mendeley.com/datasets/dyf6pnntt2/1.

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Contributions by the Authors
S.R.W. designed and performed the experiment with support from N.C.E. S.R.W. wrote the manuscript in consultation with N.C.E.

Conflict of Interest
None declared.

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Literature Cited
Abbott RJ. 1992. Plant invasions, interspecific hybridization and the evolution of new plant taxa. Trends in Ecology & Evolution 7:401–405.
Agrawal AA, Strauss SY, Stout MJ. 1999. Costs of induced responses and tolerance to herbivory in male and female fitness components of wild radish. Evolution 53:1093–1104.
Arrigo N, de La Harpe M, Litsios G, Zozomová-Lihová J, Španiel S, anonymous reviewers for helpful comments. We would also like to thank Maureen Stanton, Jodie Holt and two anonymous reviewers for helpful comments.

Barker MS, Arrigo N, Baniaga AE, Li Z, Levin DA. 2016. On the relative abundance of autopolyploids and allopolyploids. American Journal of Botany 103:1348–1357.
Ayres D, Ryan FJ, Grotkopp E, Bailey J, Gaskin J. 2009. Tumbleweed (Salsola), Chenopodiaceae: minority cytotype exclusion and barriers to triploid formation. American Journal of Botany 92:1827–1835.
Barker MS, Arrigo N, Baniaga AE, Li Z, Levin DA. 2016. On the relative abundance of autopolyploids and allopolyploids. The New Phytologist 210:391–398.
Borger CZ, Yan G, Scott JK, Walsh MJ, Powles SB. 2008. Salsola tragus or S. australis (Chenopodiaceae) in Australia—untangling taxonomic confusion through molecular and cytogenetic analyses. Australian Journal of Botany 56:600.
Bretagnolle F, Thompson JD, Lumaret R. 1995. The influence of seed size on seed germination and seedling vigour in diploid and tetraploid Dactylis glomerata L. Annals of Botany 76:607–615.
Burton TL, Husband BC. 1999. Population cytotype structure in the polyploid Galax urceolata (Diapensiaceae). Heredity 82:381–390.
Chen ZJ. 2010. Molecular mechanisms of polyploidy and hybrid vigor. Trends in Plant Science 15:57–71.
Chen ZJ. 2013. Genomic and epigenetic insights into the molecular bases of heterosis. Nature Reviews Genetics 14:471–482.
Devlin B, Clegg M, Eilstrand NC. 1992. The effect of flower production on male reproductive success in wild radish populations. Evolution 46:1030–1042.
Ehrendorfer F. 1980. Polyploidy and distribution. In: Polyploidy. Boston, MA: Springer US, 45–60.
Eilstrand NC, Schierenbeck KA. 2000. Hybridization as a stimulus for the evolution of invasiveness in plants? Proceedings of the National Academy of Sciences of the United States of America 97:7043–7050.
Fowler NL, Levin DA. 2016. Critical factors in the establishment of allopolyploids. American Journal of Botany 103:1236–1251.
Gallego-Tévar B, Rubio-Casal AE, de Cires A, Figueroa E, Grewell BJ, Castillo JM. 2018. Phenotypic plasticity of polyploid plant species promotes transgressive behaviour in their hybrids. AoB PLANTS 10:py055; doi:10.1093/aobpla/py055.
Garbutt K, Bazzaz F. 1983. Leaf demography, flower production and biomass of diploid and tetraploid populations of Phlox drummondii Hook. on a soil moisture gradient. The New Phytologist 93:129–141.
Google Earth Pro. 2015. Google Earth Pro. Grant V. 1981. Plant speciation. New York, NY: Columbia University Press.
Hegde SG, Nason JD, Clegg M, Eilstrand NC. 2006. The evolution of California’s wild radish has resulted in the extinction of its progenitors. Evolution 60:1187–1197.
Heiser CB, Whitaker TW. 1948. Chromosome number, polyploidy, and growth habit in California weeds. American Journal of Botany 35:179–186.
Holm LG. 1997. World weeds: natural histories and distribution. Wiley.
Hrusa GF, Gaskin JP. 2008. The Salsola tragus complex in California (Chenopodiaceae): characterization and status of Salsola australis and the autochthonous allopolyploid Salsola rymni sp. Madroño 55:113–131.
Husband BC. 2000. Constraints on polyploid evolution: a test of the minority cytotype exclusion principle. Proceedings of the Royal Society of London Series B: Biological Sciences 267:217–223.
Jiao Y, Wickett NJ, Ayyampalayam S, Chanderbali AS, Chanderbali AS, Landherr L, Ralph PE, Husband BC. 2000. Constraints on polyploid evolution: a test of the minority cytotype exclusion principle. Proceedings of the Royal Society of London Series B: Biological Sciences 267:217–223.
Jiao Y, Wickett NJ, Ayyampalayam S, Chanderbali AS, Chanderbali AS, Landherr L, Ralph PE, Husband BC. 2000. Constraints on polyploid evolution: a test of the minority cytotype exclusion principle. Proceedings of the Royal Society of London Series B: Biological Sciences 267:217–223.
Jiao Y, Wickett NJ, Ayyampalayam S, Chanderbali AS, Chanderbali AS, Landherr L, Ralph PE, Husband BC. 2000. Constraints on polyploid evolution: a test of the minority cytotype exclusion principle. Proceedings of the Royal Society of London Series B: Biological Sciences 267:217–223.
Jiao Y, Wickett NJ, Ayyampalayam S, Chanderbali AS, Chanderbali AS, Landherr L, Ralph PE, Husband BC. 2000. Constraints on polyploid evolution: a test of the minority cytotype exclusion principle. Proceedings of the Royal Society of London Series B: Biological Sciences 267:217–223.
Jiao Y, Wickett NJ, Ayyampalayam S, Chanderbali AS, Chanderbali AS, Landherr L, Ralph PE, Husband BC. 2000. Constraints on polyploid evolution: a test of the minority cytotype exclusion principle. Proceedings of the Royal Society of London Series B: Biological Sciences 267:217–223.
Jiao Y, Wickett NJ, Ayyampalayam S, Chanderbali AS, Chanderbali AS, Landherr L, Ralph PE, Husband BC. 2000. Constraints on polyploid evolution: a test of the minority cytotype exclusion principle. Proceedings of the Royal Society of London Series B: Biological Sciences 267:217–223.
Jiao Y, Wickett NJ, Ayyampalayam S, Chanderbali AS, Chanderbali AS, Landherr L, Ralph PE, Husband BC. 2000. Constraints on polyploid evolution: a test of the minority cytotype exclusion principle. Proceedings of the Royal Society of London Series B: Biological Sciences 267:217–223.
Jiao Y, Wickett NJ, Ayyampalayam S, Chanderbali AS, Chanderbali AS, Landherr L, Ralph PE, Husband BC. 2000. Constraints on polyploid evolution: a test of the minority cytotype exclusion principle. Proceedings of the Royal Society of London Series B: Biological Sciences 267:217–223.
Jiao Y, Wickett NJ, Ayyampalayam S, Chanderbali AS, Chanderbali AS, Landherr L, Ralph PE, Husband BC. 2000. Constraints on polyploid evolution: a test of the minority cytotype exclusion principle. Proceedings of the Royal Society of London Series B: Biological Sciences 267:217–223.
Jiao Y, Wickett NJ, Ayyampalayam S, Chanderbali AS, Chanderbali AS, Landherr L, Ralph PE, Husband BC. 2000. Constraints on polyploid evolution: a test of the minority cytotype exclusion principle. Proceedings of the Royal Society of London Series B: Biological Sciences 267:217–223.
Rieseberg LH, Raymond O, Rosenthal DM, Lai Z, Livingstone K, Nakazato T, Durphy JL, Schwarzbach AE, Donovan LA, Lexer C. 2003. Major ecological transitions in wild sunflowers facilitated by hybridization. Science 301:1211–1216.

Sabara HA, Kron P, Husband BC. 2013. Cytotype coexistence leads to triploid hybrid production in a diploid-tetraploid contact zone of Chamerion angustifolium (Onagraceae). American Journal of Botany 100:962–970.

Santos-Del-Blanco L, Bonser SP, Valladares F, Chambel MR, Climent J. 2013. Plasticity in reproduction and growth among 52 range-wide populations of a Mediterranean conifer: adaptive responses to environmental stress. Journal of Evolutionary Biology 26:1912–1924.

Scarpino SV, Levin DA, Meyers LA. 2014. Polyploid formation shapes flowering plant diversity. The American Naturalist 184:456–465.

Schlaepfer DR, Edwards PJ, Billeter R. 2010. Why only tetraploid Solidago gigantea (Asteraceae) became invasive: a common garden comparison of ploidy levels. Oecologia 163:661–673.

Schnitzler A, Muller S. 1998. Ecology and biogeography of highly invasive plants in Europe: giant knotweeds from Japan (Fallopia japonica and F. sachalinensis). Revue d’Ecologie (la Terre et la Vie) 53:3–38.

Solitis DE, Albert VA, Leebens-Mack J, Bell CD, Paterson AH, Zheng C, Sankoff D, Depamphilis CW, Wall PK, Soltis PS. 2009. Polyploidy and angiosperm diversification. American Journal of Botany 96:336–348.

Stebbins GL. 1947. Types of polyploids; their classification and significance. Advances in Genetics 1:403–429.

Stebbins GL. 1950. Variation and evolution in plants.

Stebbins GL. 1970. Variation and evolution in plants: progress during the past twenty years. In: Essays in evolution and genetics in honor of Theodosius Dobzhansky. Boston, MA: Springer US, 173–208.

Stebbins GL, Major J. 1965. Endemism and speciation in the California flora. Ecological Monographs 35:1–35.

Tani N, Tsumura Y, Fukasawa K, et al. 2012. Male fecundity and pollen dispersal in hill dipterocarps: significance of mass synchronized flowering and implications for conservation. Journal of Ecology 100:405–415.

Treier UA, Broennimann O, Normand S, Guisan A, Schaffner U, Steinger T, Müller-Schärer H. 2009. Shift in cytotype frequency and niche space in the invasive plant Centaurea maculosa. Ecology 90:1366–1377.

Wei N, Cronn R, Liston A, Ashman TL. 2019. Functional trait divergence and trait plasticity confer polyploid advantage in heterogeneous environments. The New Phytologist 221:2286–2297.

Welles SR, Ellstrand NC. 2016a. Rapid range expansion of a newly formed allopolyploid weed in the genus Salsola. American Journal of Botany 103:663–667.

Welles SR, Ellstrand NC. 2016b. Genetic structure reveals a history of multiple independent origins followed by admixture in the allopolyploid weed Salsola ryanii. Evolutionary Applications 9:871–878.

Wendel JF. 2000. Genome evolution in polyploids. In: Plant molecular evolution. Dordrecht, The Netherlands: Springer Netherlands, 225–249.

Wendel JF. 2015. The wondrous cycles of polyploidy in plants. American Journal of Botany 102:1753–1756.

Young J. 1972. Germination and establishment of Salsola in relation to seedbed environment. I. Temperature, afterripening, and moisture relations of Salsola seeds as determined. Journal of Agronomy 64:214–218.

Young FL. 1986. Russian thistle (Salsola iberica) growth and development in wheat (Triticum aestivum). Weed Science 34:901–905.

Younginger BS, Sirová D, Cruzan MB, Ballhorn DJ. 2017. Is biomass a reliable estimate of plant fitness? Applications in Plant Sciences 5:1600094.