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VIEWPOINT

Propagule pressure and the establishment of emergent polyploid populations

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• **Background** Whereas the incidence or rate of polyploid speciation in flowering plants is modest, the production of polyploid individuals within local populations is widespread. Explanations for this disparity primarily have focused on properties or interactions of polyploids that limit their persistence.
• **Hypothesis** The emergence of local polyploid populations within diploid populations is similar to the arrival of invasive species at new, suitable sites, with the exception that polyploids suffer interference from their progenitor(s). The most consistent predictor of successful colonization by invasive plants is propagule pressure, i.e. the number of seeds introduced. Therefore, insufficient propagule pressure, i.e. the formation of polyploid seeds within diploid populations, ostensibly is a prime factor limiting the establishment of newly emergent polyploids within local populations. Increasing propagule number reduces the effects of genetic, environmental and demographic stochasticity, which thwart population survival. As with invasive species, insufficient seed production within polyploid populations limits seed export, and thus reduces the chance of polyploid expansion.
• **Conclusion** The extent to which propagule pressure limits the establishment of local polyploid populations remains to be determined, because we know so little. The numbers of auto- or allopolyploid seed in diploid populations rarely have been ascertained, as have the numbers of newly emergent polyploid plants within diploid populations. Moreover, seed production by these polyploids has yet to be assessed.

Key words: Colonization, dispersal, invasion, polyploidy, population establishment, propagule pressure, seed production.

INTRODUCTION

The frequency of polyploid speciation in flowering plants is low. It is estimated to be approximately between 15 % (Wood *et al.*, 2009) and 24 % (Barker *et al.*, 2016). Whereas speciation via ploidal shift has been quite infrequent, polyploid individuals have been generated in a multitude of plant species, with the propensity for and occurrence of polyploidization varying considerably among genotypes, populations and lineages (Husband *et al.*, 2013). Given the considerable potential for a ploidal shift, it is surprising that the evolution of full-fledged species through ploidal increase has not occurred frequently. Why is this the case? It is generally accepted that the key obstacles to the establishment and spread of newly emergent polyploids are meiotic irregularities, and reduced fertility, altered gene dosage, instantly altered physiological properties, and minority cytotype disadvantage (Levin, 1975; Husband, 2000) and competitive inferiority (Baduel *et al.*, 2018; Clark *et al.*, 2019; Mandáková *et al.*, 2019). Other obstacles may include few founding individuals or a paucity of genetic diversity in the founders (Hovick and Whitney, 2019) and reduced pollen fertility and fecundity (Levin, 2002; Huynh *et al.*, 2020). Finally, polyploids may not perform well in their progenitor's habitats (Maceira *et al.*, 1993; McIntyre and Strauss, 2017; Hülber *et al.*, 2018).

In contrast to properties or interactions of polyploids, I propose that insufficient production of polyploid seeds within local diploid populations constitutes an important, perhaps prime, factor limiting the establishment of persistent polyploid populations in suitable sites. To be sufficient the seed rain would have to be substantial within 1 year or the lifetime of the seeds. If diploid populations produced many polyploid seeds, but if they were well dispersed in time, the number of potential mates at any given time would be few, and the polyploid population would be below the minimum size for persistence.

The premise that insufficient polyploid seed production is a key factor in constraining polyploid establishment is based on the similarity between newly emergent polyploids within diploid populations and founders of new populations by invasive species. Like invasive colonists, these polyploids have the potential to establish local populations where they have never previously existed. Polyploid seeds are 'imported' from their local diploid progenitors, whereas seeds of an invasive plant population are imported from extraneous populations. Polyploids also are similar to invasive species in that their long-term persistence requires the availability of suitable sites and geographical expansion. Both polyploids and invasive species require a substantive number of seeds for successful local establishment at suitable sites. It should be noted that invasive species

are preadapted to environments similar to those from which they emigrated, whereas polyploids may be less well adapted than resident diploids (Levin, 2002). If polyploids were maladapted, even copious seed production would not suffice for their establishment.

PROPAGULE PRESSURE IN INVASIVE SPECIES

The most consistent predictor of successful colonization by invasive plants is propagule pressure, the number of individuals introduced during a single colonization event (Williamson, 1996; Lockwood *et al.*, 2005; Colautti *et al.*, 2006; Simberloff, 2009; Blackburn *et al.*, 2015). Increasing propagule number increases the probability of establishment principally by reducing the effects of genetic, environmental and demographic stochasticity (Fauvergue *et al.*, 2012; Lande, 1988, 1993). Propagule pressure best predicts invasion success when establishment does not require significant evolutionary change (Peniston *et al.*, 2019). The invasion of South Africa's Agulhas Plain by woody species is better explained by propagule pressure than by specific environmental factors (Rouget and Richardson, 2003). The number of invaders introduced into riparian plots in southern California had a greater influence on invader numbers than did the richness of the resident species (Levine, 2000). Propagule pressure also is the fundamental driver of the invasion of *Opuntia stricta* in South Africa (Foxcroft *et al.*, 2004) and *Holcus lanatus* into California (Thomsen *et al.*, 2006). Most introductions to novel habitats by invasive plants fail in part because the immigration rate to suitable sites is too low (Lockwood *et al.*, 2005; Zenni and Nuñez, 2013).

Cassey *et al.* (2018) evaluated the relationship between propagule pressure and establishment success for a broad range of taxa and life histories, including herbaceous plants and long-lived trees. They found a positive mean effect of propagule pressure on establishment success in every hypothesis tested and across experimental studies. Establishment probability is low for founding populations of ten or fewer individuals and highly likely as the number approaches 100. The strong effect of propagule number occurs in spite of location-level and species-level forces that can influence establishment success.

A continuing and substantive rain of seeds, particularly from a variety of sources, may enhance the likelihood of successful colonization because larger founder populations tend to contain more genetic and phenotypic diversity (Lande, 1988; Lockwood *et al.*, 2005; Dlugosch and Parker, 2008; Fauvergue *et al.*, 2012; Luque *et al.*, 2016). Larger founder populations may contain increased genetic diversity, which may enhance colonization success. Increased diversity may increase rates of adaptation after introduction (Clegg and Allard, 1972; Reznick and Ghalambor, 2001) and reduce the level of inbreeding depression (Hufbauer *et al.*, 2013). Increased diversity in self-incompatibility alleles will increase the number of potential mates. Even if genetic diversity is very low, small populations founded by high-performing colonists may still be successful due to their ability to self-fertilize (Siopa *et al.*, 2020) or through the occurrence of genotypes whose critical population densities are low (de Groot *et al.*, 2012; Sinclair *et al.*, 2019).

Populations founded with the same number of individuals can vary substantially in their growth and persistence (Vahsen *et al.*, 2018). Dependent variables are the extent of adaptedness to the new site (e.g. Hufbauer *et al.*, 2012), how diverse founding groups are (e.g. Crawford and Whitney, 2010; Szucs *et al.*, 2014), native range size (Schmidt *et al.*, 2017) and the timing and frequency of discrete introduction events (e.g. Grevstad, 1999; Shea and Possingham, 2000). Establishment probability also is a function of the number of introductions. A continuing rain of seeds, particularly from a variety of sources, may enhance the likelihood of success (Simberloff, 2009). That a sparse seed rain is responsible for the failure of species recruitment into suitable sites has been demonstrated in seed addition and seed-trap studies in temperate (Turnbull *et al.*, 2000; Foster and Tilman, 2003; Foster *et al.*, 2004) and tropical communities (Dalling *et al.*, 2002; Makana and Thomas, 2004; Svenning and Wright, 2005).

PROPAGULE PRESSURE IN POLYPLOIDS

Following the invasive species model, the number of seeds produced in a given diploid population ostensibly is a key factor in the initial establishment of a polyploid, as is the growth of the new population. The 'invasion' of a diploid population by a polyploid is not a single-season event. Rather, polyploids may be introduced as long as the diploid is present, which could be several years or only a few years in the case of weedy species. The polyploid seed rain is expected to vary in time, being a function of diploid population size and unreduced gamete production. There may be several pulses of high polyploid seed production, a few episodes, or none. A 'drizzle' of polyploid seeds is unlikely to yield a self-sustaining population, whereas pulses may. Unreduced gamete formation typically averages from 0.1 to 2.0 % in natural populations (Bretagnolle, 2001; Mason and Pires, 2015; Kreiner *et al*., 2017*a, b*). Different diploid populations would have different numerical dynamics and patterns of environmental stress, so that the propagule pressure certainly would vary among them in time and space. The greater the number of diploid populations and the larger their sizes, the higher is the probability that polyploid production would be sufficient for their establishment somewhere in the range of their diploid antecedents.

Unfortunately, our knowledge of the polyploid seed rain is extremely limited. No tetraploids were recovered in a sample of 6000 seeds in a diploid population of *Anthoxanthum alpinum*, but a few triploids were (three per thousand; Bretagnolle, 2001). The rate of hexaploid formation in the tetraploid *Achillea borealis* was 0.428 % (Ramsey, 2007). Hexaploid seeds have been produced in agricultural autotetraploid populations such as *Beta vulgaris* (2 %; Hornsey, 1973). Given a rate of 0.004 for the production of unreduced gametes, Ramsey and Schemske (1998) estimated that the rate of autotetraploid formation would be approximately two in 100 000. This estimate is of the same order (10^{-5}) as those of the genic mutation rate obtained from studies in many organisms. These considerations indicate that a very large of number of seeds produced within a generation would be required for the establishment of polyploid populations. It follows that only very large diploid populations would host autopolyploid establishment. Large numbers of diploid hybrids would be required to produce the requisite number of allotetraploid seeds.

The production of allopolyploid seeds within diploid populations is a function of many variables, including the sizes of the two diploid species' populations, as well as their phenological similarity and cross-compatibility, the viability of their hybrids, and the penchant of the latter to produce unreduced gametes. Allopolyploid production also would be correlated with the spatial proximity of the species and the frequency of hybridization. Given that two species hybridize frequently, allopolyploid seeds are more likely to be produced than autopolyploid seeds (Ramsey and Schemske, 1998). However, populations of most diploids do not have cross-compatible relatives growing within pollination range, so the incidence of hybridization must be very low, perhaps as low as 5 % (Marques *et al.*, 2017).

Data on allopolyploid production are very sparse. From greenhouse studies, Grant (1952) estimated that the rate of polyploid production in hybrids of *Gilia millefoliata* and *G. achilleaefolia* was roughly 1.0 amphiploid per individual in 1949 and 0.18 amphiploids in 1951. The F_1 hybrids between *G. clokeyi* and *G. mexicana* yielded 0.67 tetraploids per plant, and those between *G. clokeyi* and *G. aliquanta* yielded two tetraploids per plant (Grant, 2002). Marshall and Abbott (1980) estimated that the frequency of triploid hybrid formation between the diploid *Senecio squalidus* and the tetraploid *S. vulgaris* was 0.0126 %, based on 15 861 progeny tests. This triploid is the progenitor of the hexaploid *S. cambrensis*.

Given the production of polyploid seed, how many plants within a population are newly emergent polyploids? This question is most difficult to answer, in part because it usually is impossible to discern which polyploids are of immediate origins and which ones were produced in earlier years. Taking advantage of a difference in genome size between newly formed (neo)tetraploids and long-established tetraploids, Čertner *et al.* (2017) estimated the percentage of neotetraploids in numerous (1209) populations of *Tripleurospermum inodorum* that contained diploids and long-established tetraploids. Neotetraploids constituted only 0.03 % of all tetraploids; they occurred solitarily.

Once a diploid population contains some polyploid plants and the site remains hospitable, polyploid persistence depends on their seed production; this will be a function of plant number and vigour, competitive interactions and the breeding system. The more seeds produced, the higher the probability that polyploids will persist. Reproduction without the requirement for outcrossing will increase the level of seed production. Partial selfing increases the probability that newly founded populations persist because population sizes will increase faster and perhaps to a greater extent than with cross-breeding (Pannell *et al.*, 2015). Self-fertility mitigates the minority cytotype mating disadvantage faced by rare polyploids (Levin, 1975).

Some polyploids have a penchant for asexual reproduction, which may increase the potential for population establishment and persistence in times of low seed production (Hörandl, 2006; Robertson *et al.*, 2010; Kolář *et al.*, 2017; Van Drunen and Husband, 2019). Chromosome doubling may enhance the level of asexual reproduction already present in a progenitor. Consider the tetraploid *Sorghum halepense* ($2n = 40$), which arose through hybridization between *S. bicolor* ($2n = 20$), an annual, and the perennial *S. propinquum* ($2n = 20$). Rhizomes of *S. halepense* are more extensive than those of its rhizomatous progenitor *S. propinquum* (Paterson *et al.*, 2020). The extent to which asexual reproduction facilitates the establishment of newly formed polyploids in local populations remains to be determined.

CONCLUSIONS

It is important to understand the factors influencing the establishment of polyploids in local diploid populations, because this process is a prime step in the evolution of a new species. Invasive species provide valuable insights into factors most important in polyploid establishment (Levin, 2019). Studies of invasive species indicate that the establishment of newly emergent polyploids initially is very likely contingent upon an adequate seed rain from diploids and the availability of suitable sites. The potential superiority of polyploids is irrelevant in this process; if they do not establish a persistent foothold and export seeds to suitable sites the lineage will most likely disappear.

Unfortunately, there is a dearth of knowledge about the importance of propagule pressure, which is pivotal in polyploid establishment. Hovick and Whitney (2019) investigated the relationship between propagule pressure and the likelihood of population persistence in a seed addition experiment using *Arabidopsis thaliana*. They demonstrated that the positive effect of propagule pressure lasted for only three generations, and subsequently was dependent on numerous factors. There is no corresponding information on strictly outcrossing species, whose initial populations may experience Allee effects and inbreeding depression (Kramer *et al.*, 2009; Szucs *et al.*, 2014).

There is a huge disparity between what we know about invasives and polyploids. We know very little about polyploid seed production by diploid plants, and the number of polyploid plants arising from such. If the successful transitions from diploidy to polyploidy were based in part on propagule pressure, then we should study species in which this transition has occurred multiple times. Consider first an example involving autotetraploids. *Galax urceolata*, which is a herbaceous, self-incompatible perennial, has arisen independently at least 46 times (Servick *et al.*, 2015). This is among the highest frequencies of independent polyploidizations known for an auto- or allopolyploid. There are numerous questions that can be asked about this species relative to the thesis of the paper. How many tetraploid seeds are produced by diploid plants, and to what extent does it vary among plants and populations? How many tetraploid plants occur within diploid populations? How many seeds do tetraploid plants produce, and to what extent does the number vary among plants and populations?

Populations containing pairs of *Tragopogon* species (*T. dubius*, *T. pratensis*, *T. porrifolius*) and their tetraploid derivatives (*T. mirus* derived from *P. porrifolius* and *T. dubius*; *T. miscellus* derived from *T. pratensis* and *T. dubius*) would be excellent venues for assessing the early ingredients of allotetraploid success. The tetraploids are the products of multiple independent origins within the past century (Soltis *et al.*, 2004). The diploid species occur jointly at some locations, as do tetraploids and their progenitors. Both allotetraploids form numerous populations, some with thousands of plants (Novak *et al.*, 1991). Some of the questions that could be asked of this system are as follows. How many

seeds of each parental species are F_1 hybrids? How many tetraploid seeds do the hybrids produce? How many hybrids are present in natural populations? How many tetraploids are present in natural populations? How many seeds do tetraploid plants produce? Empirical estimates (available and to be obtained) should shed light on the paradoxical paucity of neopolyploids in natural populations and on the regularity of multiple origins as judged from molecular surveys.

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